

Sexual Dimorphism in the Face of *Australopithecus africanus*

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ABSTRACT Recently discovered crania of *Australopithecus africanus* from Sterkfontein Member 4 and Makapansgat enlarge the size range of the species and encourage a reappraisal of both the degree and pattern of sexual dimorphism. Resampling methodology (bootstrapping) is used here to establish that *A. africanus* has a greater craniofacial size range than chimpanzees or modern humans, a range which is best attributed to a moderately high degree of sexual dimorphism. Compared to other fossil hominins, this variation is similar to that of *Homo habilis* (sensu lato) but less than that of *A. boisei*. The finding of moderately high dimorphism is corroborated by a CV-based estimate and ratios between those specimens considered to be male and those considered to be female. Inferences about the pattern of craniofacial dimorphism in the *A. africanus* face currently rely on the relationship of morphology and size. Larger specimens, particularly Stw 505, show prominent superciliary eminences and glabellar regions, but in features related in part to canine size, such as the curvature of the infraorbital surface, large and small specimens of *A. africanus* are similar. In this respect, the pattern resembles that of modern humans more so than chimpanzees or lowland gorillas. *A. africanus* may also show novel patterns of sexual dimorphism when compared to extant hominines, such as in the form of the anterior pillar. However, males of the species do not exhibit characteristics of more derived hominins, such as *A. robustus*. *Am J Phys Anthropol* 108:97–127, 1999.

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Sexual dimorphism is a focus of study in the hominoid fossil record because it may provide rare insight into the social behavior of fossil animals. Dimorphism in body size and/or canine size has been shown to be related to some aspects of social structure in modern primates (Leutenegger and Kelley, 1977; Leutenegger and Cheverud, 1985; Gaulin and Sailer, 1984; Foley and Lee, 1989; Plavcan and van Schaik, 1992, 1994, 1997; Mitani et al., 1995). Accordingly, inferences about sexual dimorphism in the fossil record have usually drawn on overall body weight as inferred from postcranial specimens (McHenry, 1986, 1991; Jungers, 1988;

Lovejoy et al., 1989; Ruff et al., 1989; Plavcan and van Schaik, 1997) or the size of the dentition, especially the canine (Robinson, 1956; Wolpoff, 1975; Kay, 1982; Leutenegger and Shell, 1987; Kimbel and White, 1988; Kelley and Xu, 1991; Kelley, 1993; Plavcan and van Schaik, 1997).

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Sexual dimorphism in the cranium is of interest mainly because of its relevance to systematics. Given variation in a sample of fossil hominins,¹ the conclusions of two sexes or two species are often counterpoised. One prominent example of this approach is the analysis of variation in *Homohabilis* (sensu lato) (Wood, 1985, 1991, 1993; Stringer, 1986; Lieberman et al., 1988; Miller, 1991; Tobias, 1991; Rightmire, 1993; Kramer et al., 1995; Grine et al., 1996). Studies of sexual dimorphism in modern hominine skulls have provided the necessary background to explore patterns of dimorphism in fossil taxa using both univariate and multivariate methods (Wood, 1976; O'Higgins et al., 1990; Wood et al., 1991; O'Higgins and Dryden, 1993). O'Higgins et al. (1990:417) suggested that while "differences in sexual dimorphisms between hominoids are generally smaller than the similarities which exist between them," patterns of sexual dimorphism differ in identifiable ways between species or between human populations.

Patterns of dimorphism may also be differentiated from the degree of dimorphism. The phrase "degree of sexual dimorphism" seems to imply that a species displays a uniform pattern of sexual dimorphism, an assumption which is known to be false. Nonetheless, samples drawn from single species do possess an average level of sexual dimorphism for any trait or set of traits, from which individual characters and measurements may deviate. Thus, the *degree* and *pattern* of sexual dimorphism are separable quantities that, in reference to a series of dimensions, I regard as analogous to the *size* and *shape* of a variability profile (Sokal and Braumann, 1980). In fossil samples, the overall degree of variation can be approximated through distributional statistics and used to make inferences about the degree of sexual dimorphism. An example of a pattern of dimorphism is the unusual combination of high body size dimorphism and low canine size dimorphism in *Australopithecus afarensis*

(for discussion see Plavcan and van Schaik, 1997).

The goal of this study is to examine the craniofacial sexual dimorphism of *A. africanus* in a comparative context. Most authors recognize *A. africanus* as the only hominin taxon in the Sterkfontein Member 4 and Makapansgat deposits. Ongoing excavations by the University of the Witwatersrand at Sterkfontein have substantially increased the available sample and its variation (Tobias and Baker, 1994). The unity of the *A. africanus* hypodigm is debatable (Clarke, 1988, 1994a; Kimbel and White, 1988; Lockwood, 1997; Moggi-Cecchi et al., 1998). However, most of the adult specimens probably do comprise one species (Lockwood, 1997; Lockwood and Tobias, submitted). In addition, one method of testing the hypothesis that the adult craniofacial remains from Sterkfontein Member 4 and Makapansgat belong to a single species is to analyze the degree and pattern of sexual dimorphism that is implied if those specimens are grouped together. Therefore, this study adopts a conservative and broad definition of *A. africanus* (see Materials).

Quantitative and qualitative approaches are chosen to address several issues. Modern hominines are examined to establish the extent to which the degree and pattern of craniofacial dimorphism are separable when sex is known as well as to identify morphological correlates of these patterns that might facilitate the interpretation of pattern in fossil hominins. In a fossil species such as *A. africanus*, the first question is whether size variation is great enough to justify the identification of sex in part on the basis of size. In other words, is size variation in *A. africanus* greater than expected for weakly dimorphic species such as modern humans or chimpanzees? If so, what aspects of facial morphology in *A. africanus* are developed in larger, presumably male individuals? Finally, does sexual dimorphism in *A. africanus* bear upon the origin of the modern human pattern of craniofacial dimorphism?

MATERIALS

Modern hominines

The extant hominine reference samples (Table 1) consist of Zulu crania and mixed-

¹As used here, "hominin" refers to a member of the tribe that includes modern humans and all extinct taxa more closely related to modern humans than to any other extant taxa, following Groves (1989) and others. The subfamily Homininae includes gorillas, chimpanzees, humans, and all descendants of their common ancestor.

TABLE 1. Extant hominine adult crania in the comparative sample

Species	Group	Male	Female	Total	Source ¹
<i>Homo sapiens</i>	Zulu	32	32	64	UW
<i>Gorilla gorilla</i>	<i>gorilla</i>	20	18	38	AMNH, SI
	<i>beringei</i>	14	9	23	SI, UW
	Total	34	27	61	
<i>Pan troglodytes</i>	<i>troglodytes</i>	12	13	25	AMNH, MCZ, SI
	<i>schweinfurthii</i>	8	4	12	AMNH, SI, UW
	<i>verus</i>	7	10	17	AMNH, HAR, MCZ, SI
	unspecified	4	5	9	AMNH, MCZ, UW
	Total	31	32	63	

¹ AMNH, American Museum of Natural History, New York; HAR, Department of Anthropology, Harvard University; MCZ, Museum of Comparative Zoology, Harvard University; SI, Smithsonian Institution, Washington, DC; UW, Department of Anatomical Sciences, University of the Witwatersrand, Johannesburg. Not all specimens are used in every analysis.

subspecies samples of gorillas and chimpanzees. The age range for the Zulu specimens used here is given as 19–68 from records of the Dart Collection at the University of the Witwatersrand, Johannesburg, South Africa. For the apes, the sex of most specimens had been determined in the field, but to increase the sample size I utilized a few specimens for which canine size had been used by curators to assign sex. All great ape specimens are adult, to judge by the occlusal position of M³.

The chimpanzee sample contains stated representatives of all three subspecies of *Pan troglodytes* and some wild-shot specimens with no locality data. The sample clearly encompasses a wide degree of geographical variation, but results from other studies (e.g., Shea et al., 1993) suggest that the subspecies of *P. troglodytes* are very similar in cranial form. Because of some size differences among the subspecies, the combined sample is a conservative portrayal of size variation in a species. Some have argued that pooling subspecies in a comparative sample is appropriate as one way to simulate the sampling of fossil species through time (e.g., Richmond and Jungers, 1995).

The subspecies of *Gorilla gorilla* used here, *G. g. gorilla* and *G. g. beringei*, are distinct on both morphological (Schultz, 1934; Vogel, 1961; Groves, 1970; Uchida, 1992, 1998) and molecular grounds (Ruvolo et al., 1994). These samples are separated for the analysis of modern hominine patterns of dimorphism. They are combined for the resampling section of the study, as explained below.

Fossil specimens

The fossil sample of faces from Sterkfontein Member 4 and Makapansgat Member 3 consists of thirteen adults upon which at least one of the measurements discussed below can be made: TM 1511, TM 1512, Sts 5, Sts 17, Sts 53, Sts 63, Sts 71, Sts 3009, Stw 13, Stw 73/22, Stw 505, MLD 6/23, MLD 9. These are included in the quantitative analyses. Several more fragmentary or immature specimens are also useful for morphological comparisons. These are TM 1514, Sts 52 (immature), Stw 391 (possibly immature), Stw 498 (immature), and MLD 45.

The Stw specimens were excavated by the University of the Witwatersrand under the direction of P.V. Tobias and A.R. Hughes and are presently undescribed. While this study does adopt a broad definition of *A. africanus*, including several Stw specimens, I do not discuss Stw 183 and Stw 252, two immature individuals. These specimens may provide evidence of a second species in Sterkfontein Member 4 but require further interpretation on their own (Clarke, 1988; Lockwood, 1997; Lockwood and Moggi-Cecchi, 1998). Because they are immature, their exclusion does not affect this analysis, which is based primarily on adults.

Among the Stw specimens, Stw 13 is a crushed partial adult cranium with some teeth. The face is more complete than the fragmentary calvaria, but distortion is clear in places. Better preserved but less complete is Stw 73/22 (hereafter referred to as Stw 73), the lower part of a well-preserved adult maxilla with most of the postcanine dentition. Stw 22 makes up the left M1 and M2 of

the same specimen. Both Stw 13 and Stw 73, though undescribed, have seen extensive discussion in other publications (e.g., Rak, 1983; Tobias, 1991). They are from the Member 4 breccia.

Also from Member 4 is Stw 505, a largely complete cranium with heavily damaged dentition (Lockwood and Tobias, submitted). The specimen retains most of the face with varying amounts of distortion.

Stw 391 and Stw 498 are among those Stw specimens found in situ at Sterkfontein from decalcified breccia south of the old Type Site or Member 4 and east of the Extension Site or Member 5. Provenience was uncertain upon discovery because the Member 4–Member 5 boundary is unclear in the decalcified breccia. Recent studies of Sterkfontein stratigraphy (Clarke, 1985, 1994b; Partridge and Watt, 1991) suggest that these specimens are well within the probable boundaries of Member 4.

Stw 391 is a small, well-preserved fragment of a right anterior maxilla with the roots of P3 and P4. Stw 498 consists of the lower parts of the left and right maxillae, with the complete left permanent dentition in place and parts of the right dentition preserved. The left side preserves the infra-orbital region nearly to the position of the infraorbital foramen; the right side is severely crushed.

Finally, MLD 45 is an undescribed right maxillary fragment (composed largely of the anterior pillar) with the third premolar in position. It is from Makapansgat Member 3.

Some measurements on fossil specimens are estimates or are calculated by doubling a distance between a landmark and midline. These cases are indicated on the raw data tables.

METHODS

Craniofacial measurements

Twenty-eight measurements of the facial skeleton were taken where available. These are listed in Table 2 and described graphically in Figure 1 (see the appendix for measurement definitions). They form primarily four groups: facial heights, facial breadths, measurements of the maxillo-alveolar and

TABLE 2. *Craniofacial measurements*¹

Measurement	Abbreviation
Facial heights	
1. Orbital height	ORBH
2. Glabellar height	GLAH
3. Upper facial height	UPFH
4. Nasal height	NASH
5. Orbito-alveolar height	OALH
6. Orbito-jugal height	OJUH
7. Foraminal height	FORH
8. Malar depth	MALH
9. Alveolar height	ALVH
Facial breadths	
10. Orbital breadth	ORBB
11. Superior facial breadth	SUFB
12. Anterior interorbital breadth	ITOB
13. Bimaxillary breadth	BMAB
14. Bizygomatic breadth	ZYGB
15. Interforaminal breadth	IFOB
16. Nasal aperture breadth	NASB
17. Snout breadth	SNOB
Maxillo-alveolar and palatal dimensions	
18. Anterior maxillo-alveolar breadth	ANMB
19. Maxillo-alveolar breadth	MAXB
20. Anterior palatal breadth	APAB
21. Palatal breadth	PALB
22. Maxillo-alveolar length	MAXL
23. Postcanine maxillo-alveolar length	PMXL
Facial projections	
24. Glabellar projection	GLAP
25. Prosthion projection	PROP
26. Zygomaxillare to porion distance	ZYMP
27. Malar root to porion distance	MALP
Other	
28. Postorbital breadth	POSB

¹ See Appendix 1 for measurement definitions.

palatal region, and facial projections. Most of these measurements are consistent with the definitions given by Martin and Knußmann (1988) or follow other workers cited in the appendix. I designed other measurements to gain more detail on the face. The four-letter abbreviations do not refer to any previous usage.

Only the left side of the face was measured in the extant groups. The preserved side was used for each fossil specimen, the average being taken when both sides were available. Only chord measurements were taken, and sliding digital calipers were used throughout. Values were recorded to the nearest 0.1 mm on all specimens.

In order to determine measurement reliability, five human crania were measured three times each at greater than 2 month intervals. The average deviation of the three repetitions from the mean was then calculated for each variable. The highest error

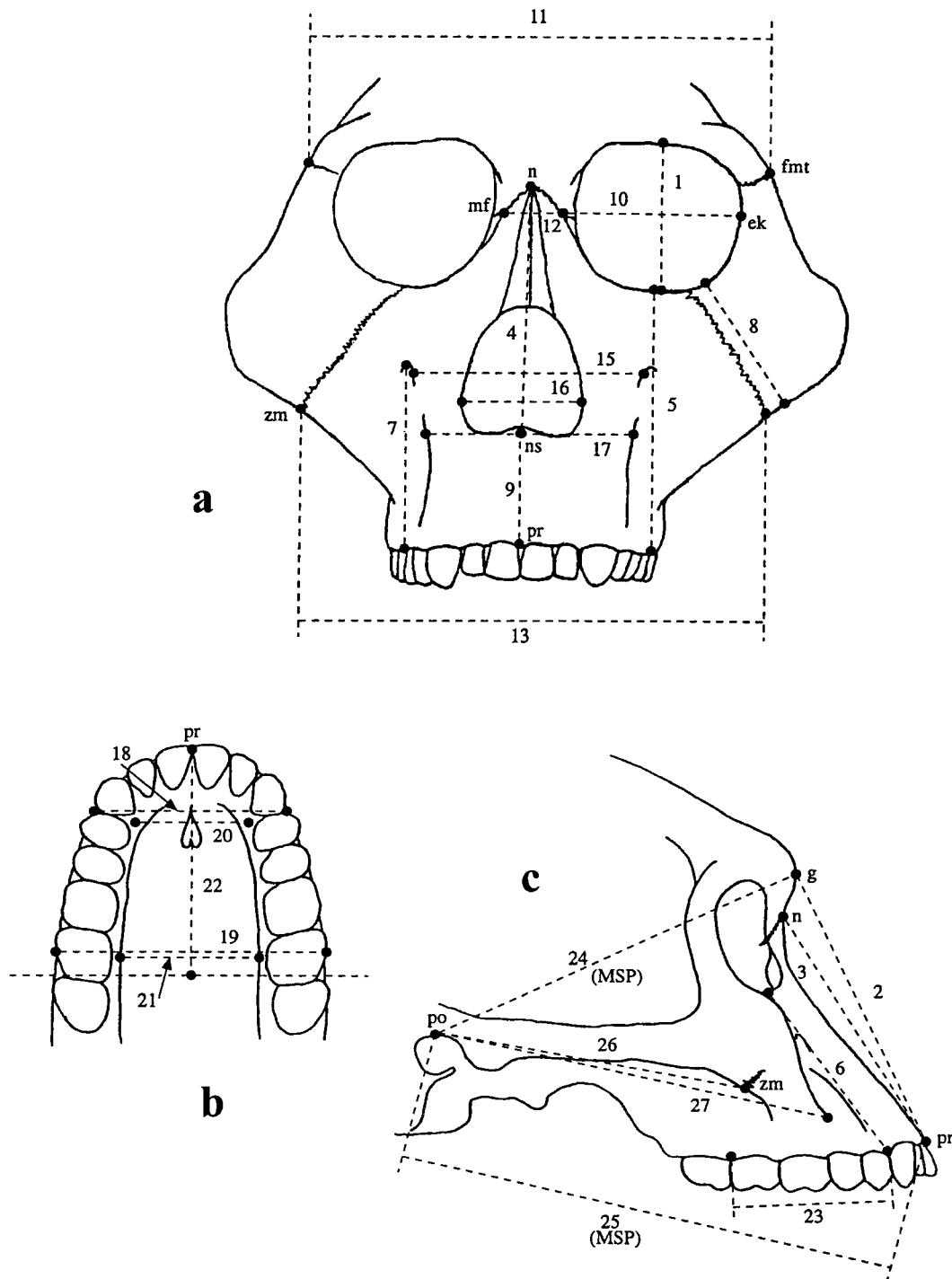


Fig. 1. Measurements of the face. **a:** Anterior view. **b:** Palatal view. **c:** Lateral view. Numbers refer to the labels in Table 2 and the appendix, and craniometric points are defined in Martin and Knußmann (1988): *ek*, ectoconchion; *fmt*, frontomale temporale; *g*, glabella; *mf*, maxillofrontale; *n*, nasion; *ns*, nasospinale; *po*, porion; *pr*, prosthion; *zm*, zygomaxillare. MSP (median sagittal plane) measurements were calculated as described in the appendix.

was 2.6%, but roughly two-thirds of the variables had less than a 1% error associated with them. Also, the three calculated variables (see the appendix) were as reliable as or more reliable than measurements that were directly measured (less than 0.6% error).

Quantitative methods

Modern hominines. Quantitative methods used here differ for modern and fossil hominines because sex is known in modern samples and far more complete specimens are available. For extant hominines, the degree of sexual dimorphism is assessed directly through the use of an index of sexual dimorphism (ISD). The ISD used here is the ratio of the mean value for males to the mean value for females. One is subtracted from this ratio, and the result is multiplied by 100 to ease comparisons. For example, an ISD of 8.6% indicates that for that measurement and sample the mean value for males is 8.6% larger than that for females. Because ISDs compare mean values but do not take into account intrasexual variability, the Student's *t*-test is also used to test sex differences. These *t*-tests are not independent from one another because the measurements themselves are correlated to varying degrees.

The profile of indices for each modern hominine species is used to represent its quantitative pattern of sexual dimorphism. The similarity or dissimilarity in patterns of sexual dimorphism among modern hominines is evaluated using the nonparametric Spearman's rank correlation coefficient r_s , as calculated between the lists of ISDs for two species.

Size variation in fossil taxa. Where sex is unknown in a sample, it is important to determine how well size discriminates between sexes. A high level of size variation should indicate that size dimorphism is pronounced. If so, the various methods of estimating dimorphism become more secure because all rely on size discrimination between sexes to some extent (Plavcan, 1994). Without demonstration that a fossil sample is size-dimorphic, there is little justification

for direct estimates of sexual dimorphism or further inferences about sexual dimorphism in facial morphology.

Resampling methodology (bootstrapping) following Lockwood et al. (1996) and others (Arsuaga et al., 1997; Lorenzo et al., 1998) is used here to assess size variation in fossil hominins. For each analysis of a fossil sample with sample size n , random samples of n individuals are generated from extant comparative groups in order to establish a distribution of variation that can be expected from modern analogues. In this case, the goal is to determine the probability of sampling a set of n individuals from an extant hominine species whose largest and smallest members exhibit size differences in the face greater than those present in a sample of n individuals of *A. africanus*. If the result is a very low probability (e.g., <0.05) in comparisons to species with the highest degree of craniofacial dimorphism in hominids (gorillas), this would arguably be evidence for multiple species in the *A. africanus* hypodigm—if we assume that early hominins are unlikely to exceed gorillas in the degree of craniofacial dimorphism. Low probabilities when compared to less dimorphic hominids (chimpanzees and humans) would suggest that size variation, and by inference sexual dimorphism, in *A. africanus* is higher than in those taxa.

The primary difference between the resampling methodology used here and the randomization methods used in some previous studies of fossil hominin variation (Lieberman et al., 1988; Grine et al., 1993, 1996; Richmond and Jungers, 1995; Kramer et al., 1995) is the attempt here to take into account fossil sample sizes (for different methods based on the same principle, see Kramer, 1993; Cope and Lacy, 1995; Kramer et al., 1995). The analysis is performed only for max/min comparisons because specimens in the *A. africanus* sample are preserved in different ways, and there is therefore no way to obtain a coefficient of variation (CV) for a particular surrogate of overall craniofacial size.

There are two main requirements for the max/min analysis. The first is to establish which specimens are the largest and small-

est for the sample and what measurements they share. The second is to have an estimate of the total fossil sample size for specimens that can be reliably compared in size (i.e., reasonably well-preserved craniofacial remains of mature individuals).

For *A. africanus*, the max/min analysis is performed for both Sterkfontein Member 4 alone and the pooled-site sample (Sterkfontein Member 4 and Makapansgat). Sterkfontein Member 4 may better represent a single population (unlikely, but the true extent of temporal aggregation is unknown), but in any case the pooled-site sample represents the known range of variation in adults of *A. africanus*. At Sterkfontein Member 4, 12 adult faces are sufficiently preserved to show that Stw 505 is the largest and either TM 1512 or Sts 17 the smallest² (TM 1511, TM 1512, TM 1514, Sts 5, Sts 17, Sts 53, Sts 63, Sts 71, Sts 3009, Stw 13, Stw 73, and Stw 505). Sts 17 is more complete than TM 1512 and therefore permits a more accurate determination of size variation. There are 12 variables common to Stw 505 and Sts 17: glabellar height, orbito-alveolar height, orbito-jugal height, foraminal height, alveolar height, malar depth, superior facial breadth, bimaxillary breadth, interforaminal breadth, nasal breadth, anterior maxillo-alveolar breadth, and anterior palatal breadth.

For the pooled-site sample, three specimens are added (MLD 6, MLD 9, MLD 45), so the total *n* is 15. MLD 6 is marginally smaller than Sts 17 or TM 1512 and therefore extends the size variation slightly. Stw 505 and MLD 6 share eight variables: orbito-alveolar height, orbito-jugal height, foraminal height, anterior interorbital breadth, interforaminal breadth, nasal breadth, anterior maxillo-alveolar breadth, and anterior palatal breadth.

Comparison to other early hominin species is used to give added background on hominine size variation. *H. habilis* (including KNM-ER 1470) and *A. boisei* are two species for which presumed members of both sexes have been sampled and for which the

degree of craniofacial dimorphism is probably high if each is regarded as one species (e.g., Wood, 1991). *A. robustus* is not used in this analysis because the measurable sample is small and the well-preserved specimens are of similar sizes. On present evidence, it is clear that the species was no more size-variable than modern humans or chimpanzees.

For *H. habilis*, there is much disagreement over which specimens belong to the species. Craniofacial size dimorphism is probably only a concern in *H. habilis* if large individuals such as KNM-ER 1470 are included in this taxon. Among craniofacial remains, the appropriate lower and upper extremes of size are KNM-ER 1813 and KNM-ER 1470, no matter how many specimens of intermediate size are incorporated (the face of Stw 53 is approximately the same size as that of KNM-ER 1813, depending on the variables used). Size-related comparisons have been used as evidence that specimens such as KNM-ER 1470, KNM-ER 1590, and KNM-ER 3732 belong to a different species, *H. rudolfensis* (Lieberman et al., 1988; Wood, 1991; Kramer et al., 1995; Grine et al., 1996). Therefore, the sample provides an important measure of what kinds of size variation have been considered unacceptable in previous studies of hominins. KNM-ER 1470 and KNM-ER 1813 are also among the most complete crania of *H. habilis*, and nearly all of the measurements for the current study can be obtained. The rest of the *H. habilis* sample is KNM-ER 1805, OH 24, OH 62, and Stw 53, for a total *n* of 6.

For *A. boisei*, there is widespread agreement that individuals as different in size as OH 5 and KNM-ER 732 belong to the same species (e.g., Leakey, 1971; Wood, 1991; Groves, 1989; Kimbel and Rak, 1993). KNM-ER 732 is less complete and limits the number of measurements available. Other craniofacial specimens in *A. boisei* are KNM-ER 405, KNM-ER 406, KNM-ER 13750, and KNM-WT 17400, for a total of six.

Because the measurements for each comparison vary, four combinations of variables will be used to enable comparisons of prob-

²Due to the great number of fragmentary craniofacial remains from Sterkfontein Member 4, arguments could be made to justify a resampling *n* between 10 and 14. The exact number is subjective, and, at these sample sizes, the results vary little.

TABLE 3. Variables used in resampling analyses of size variation in early hominins¹

Eight variables (a): OALH, OJUH, FORH, ITOB, IFOB, NASB, ANMB, APAB
Eight variables (b): OALH, OJUH, FORH, MALH, SUFB, BMAB, IFOB, NASB
Twelve variables: GLAH, OALH, OJUH, FORH, MALH, ALVH, SUFB, BMAB, IFOB, NASB, ANMB, APAB
Nineteen variables: ORBH, NASH, OALH, OJUH, FORH, MALH, ORBB, SUFB, ITOB, BMAB, IFOB, NASB, MAXB, PMXL, GLAP, PROP, ZYMP, MALP, POSB

¹ See Table 2 for measurement abbreviations.

abilities between species (Table 3): the eight variables (8a) shared by Stw 505, MLD 6, KNM-ER 1470, and KNM-ER 1813, the 12 variables shared by Stw 505, Sts 17, KNM-ER 1813, and KNM-ER 1470, the eight variables (8b) shared by these specimens in addition to OH 5 and KNM-ER 732, and finally the 19 variables shared by OH 5, KNM-ER 732, KNM-ER 1813, and KNM-ER 1470.

The variable used to express size is the geometric mean (Mosimann, 1970; Jungers et al., 1995). For each individual face, the geometric mean is calculated as the n th root of the product of n measurements. In cases where one or two measurements could not be taken on a modern hominine skull, these values are replaced by the arithmetic mean for the sex and species concerned.

The ratio of the geometric means between the largest and smallest specimens is used as a measure of size range. Gorilla subspecies are pooled, as the separate sample sizes are each too small to simulate population variation. In this case, both the minimum and maximum geometric means are represented by lowland gorillas, and therefore the inclusion of mountain gorillas into the sample apparently does not influence the overall range of variation.

For each set of facial variables, 1,000 random samples of geometric means are selected with replacement from the extant hominine groups. The frequency with which a sample is found whose range exceeds that of a fossil sample is reported. Clearly, if the range of a fossil sample exceeds that of the entire reference sample available here for an extant taxon, the probability of sampling

the relevant max/min ratio is 0%, and no resampling is required to demonstrate this.

Discrete estimates of sexual dimorphism in *A. africanus*. The degree of sexual dimorphism can be expressed in a relative sense using the resampling procedures described above. In addition, there are several methods to provide a discrete estimate of dimorphism where sex is unknown. Two methods are compared here. For each, the 18 measurements selected are those with sample sizes between five and 11 adults each; the large cranium Stw 505 is included in the sample of 14 of these measurements. These differ from those used in the resampling analysis of size variation because the latter is confined to those measurements shared between smallest and largest crania.

The first method of direct estimation involves the calculation of indices of sexual dimorphism based on different procedures of sex assignment. Individual specimens may be assigned sex and then used to calculate indices (cf. McHenry, 1991). This is more justified if size variation has been demonstrated to be higher than relatively monomorphic reference groups. Putative males can then be compared to putative females, and there will generally be some overlap of the distributions for each character. For the current study, the adult specimens used for *A. africanus* are MLD 9, TM 1511, Sts 5, Stw 13, and Stw 505 (putative males) and MLD 6, TM 1512, Sts 5, Stw 13, Sts 17, Sts 53, Sts 71, and Stw 73 (putative females).³ These determinations of sex are based on a combination of craniofacial size and morphology, the details of which are presented in Results and Discussion below. Sex is more uncertain for Sts 5 and Stw 13 than for other specimens, so their assignments are varied in the analysis. For one estimate (A), both are treated as males. For estimate B, only Stw 13 is treated as a male, and for estimate C, both Sts 5 and Stw 13 are considered to be females.

The second method of estimating the degree of sexual dimorphism depends on the

³The possibility remains that Stw 505, distinctly larger than other specimens, is the only adult male in the sample. If so, the estimates of dimorphism presented here are probably underestimates.

correlation of pooled-sex CVs with ISDs. The present study differs from previous, similar methodologies (Fleagle et al., 1980; Kay, 1982; Leutenegger and Shell, 1987) by averaging CVs and ISDs across a suite of variables. The mean ISD across all variables succinctly portrays the degree of sexual dimorphism in the facial skeleton, though it by definition disregards the pattern of dimorphism. This average degree has biological meaning in the same way as any other average level of variation. When dealing with small samples, the variability profile of a sample is not significantly different from a straight line at the average level of variation (Sokal and Braumann, 1980). Pattern differences in variation, or specifically sexual dimorphism, do exist but are not statistically robust.

The reduced major axis regression line that is determined in a bivariate comparison of the average ISD and average CV among extant hominines may be used to estimate sexual dimorphism in a sample where only the pooled-sex CV is known. To maintain equal proportions of males and females in the reference samples used to determine this relationship, we removed four mountain gorilla males randomly from the sample so that nine mountain gorillas of each sex are used.

Areas of study for facial morphology

Facial morphology is used here as the primary means of discussing the pattern of sexual dimorphism in *A. africanus* and to assist in sex assignment for individual crania. Variation is also examined in modern hominine samples. The focus is on several areas of morphology: the form of the supraorbital region (particularly the superciliary portion), the form and anterior prominence of glabella, the projection or hollowing of the central face, the most anterior position of the zygomatic process, and the degree of concavity of the infraorbital region. These traits are prone to vary in all species. The form of the anterior pillar (sensu Rak, 1983) is also studied in *A. africanus*, but it has no clear analogue in extant hominines.

It is noted whether specimens possess a superciliary arch—in other words, a supraor-

bital region divided into superciliary and supraorbital components in the manner described for humans by Schwalbe (1906) and Cunningham (1909). In the modern human sample and, where appropriate, early hominins of the current study, the prominence of the superciliary arch is judged to be absent, slight, moderate, or marked, after De Villiers (1968) and Morris (1984). To gauge the size of the supraorbital arch (or torus) in apes and early hominins, I measured its vertical thickness at the highest point on the superior orbital margin (Tobias 1967, 1991). No similar measurement is relevant to humans.

Guidelines for assessing the anterior prominence of the glabellar mound in humans are given by Martin and Knußmann (1988). According to these guidelines, the prominence, or curvature, of glabella in modern humans includes consideration of the frontal bone superior to glabella (see also the metrical expression of glabellar prominence in Howells, 1973). However, the frontal bone retreats more horizontally in apes and early hominins than in modern humans. In the current study, therefore, the prominence of glabella is estimated subjectively relative to sellion, the most posterior point in the midline of the facial skeleton (Bunak, 1941) (Fig. 2). Those specimens on which the most posterior point in the midline of the facial skeleton is glabella itself are characterized as receding, for in these specimens there is no true sellion. Projection of glabella from sellion in other specimens is classified as flat, slight, moderate, or marked. The presence or absence of a posterior midline depression in glabella is further noted. In specimens with this character, the point glabella lies in a shallow groove between the medial portions of the supraorbital arches.

There are primarily three components of variation in the projection or hollowing of the central face: 1) the curvature of the nasal bones themselves, 2) the anterior prominence of the frontal processes of the maxilla with which the nasal bones articulate, and 3) the anterior prominence of the facial surface of the zygomatic. Actual central facial hollows (Tobias, 1972) are restricted mainly to some early hominins and

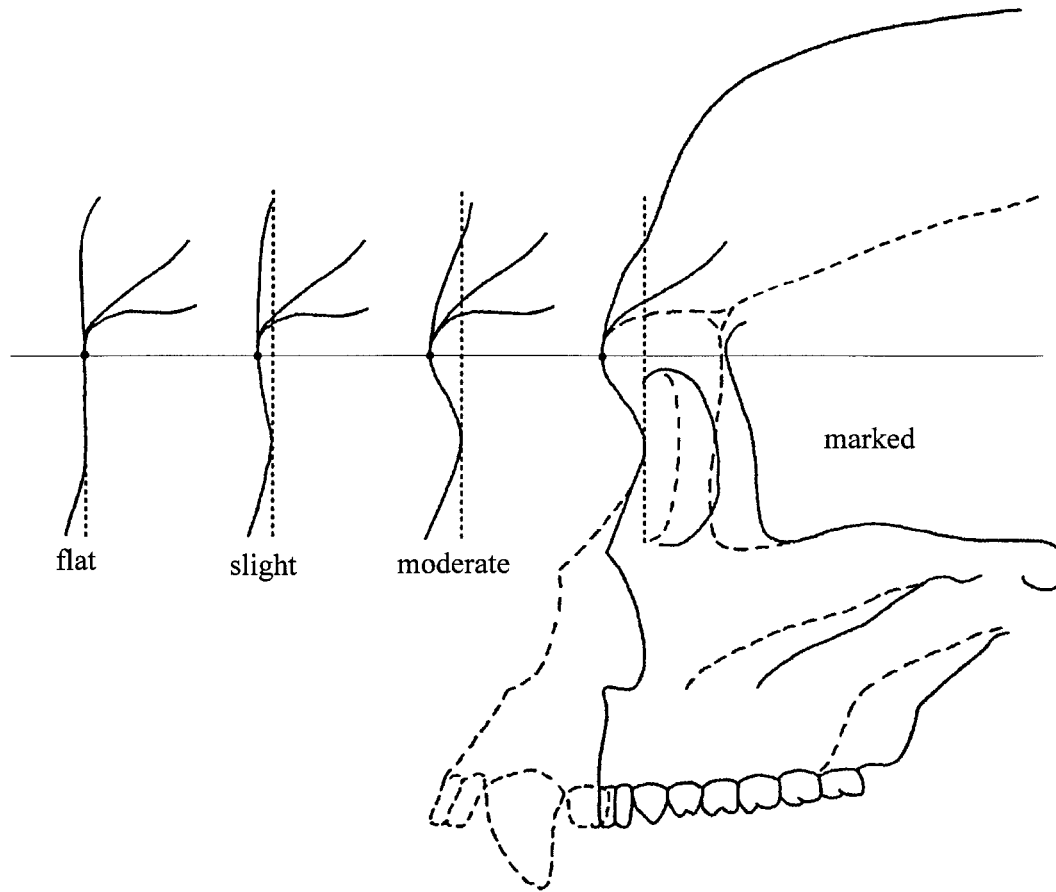


Fig. 2. Schematic representation of the categories used for the anterior prominence of glabella. The horizontal line indicates the level of glabella. The vertical line indicates the position of sellion. The different slopes of the frontal bone represent a generic African ape, an early hominin, and a modern human. Not to scale.

were important in the initial diagnosis of *Paranthropus* specimens in South Africa ("dished" faces) (Broom and Schepers, 1946; Robinson, 1961, 1962, 1968). Whether or not specimens of a particular species customarily display a central facial hollow, the variation in the components listed above may be useful in determining the pattern of variation in the central face. These are discussed for all samples but are not formally categorized or quantified in any way.

The anterior surface of the infraorbital region in hominines is curved to some degree in the sagittal and/or transverse planes (Sergi, 1947, 1960). In this study, curvatures in these planes are noted together as the degree of concavity of the infraorbital region. The infraorbital region is categorized

as flat when there is no pronounced curvature. When the infraorbital region is concave, the terms applied to the concavity are slight, moderate, and marked (Fig. 3) (see also De Villiers, 1968).

The position of the zygomatic process on the maxilla relative to the tooth row varies widely among extant and fossil hominines (Greenfield, 1979; Kimbel et al., 1984). The most anterior origin of the zygomatic process is examined here. This approach follows Kimbel et al. (1984) and differs from that of Greenfield (1979), who used the most anterior origin of masseteric fibers. The present method was chosen because the anterior limit of the zygomatic process is more often preserved in fossil specimens. The categories used to describe the zygomatic process

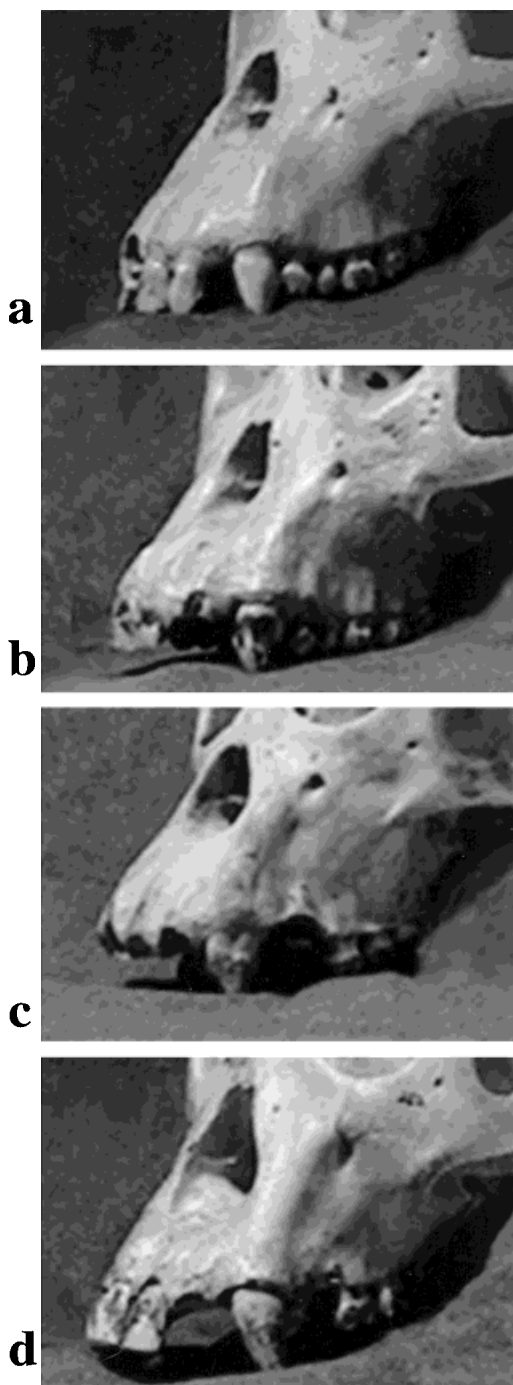


Fig. 3. A series of chimpanzees used to demonstrate variation in the concavity (or hollowing) of the infraorbital region. **a:** Flat. **b:** Slight. **c:** Moderate. **d:** Marked. Not to scale.

position refer either to an individual tooth or to the interalveolar septum between two teeth (e.g., P^3 , P^3/P^4 , P^4).

The term *anterior pillar* was suggested by Rak (1983) to represent a column of bone that forms the rounded margin of the nasal aperture and runs alongside the nasoalveolar clivus in some specimens of *A. africanus* and *A. robustus*. It is largely independent of the canine jugum. Variability in its prominence and size exists in *A. africanus*, *A. robustus*, and other species of early hominins (Rak, 1983; McKee, 1989; Tobias, 1991).

For nonmetrical traits that are formally categorized (prominence of the superciliary eminence, anterior prominence of glabella, concavity of the infraorbital region, position of the zygomatic process), sex differences in extant hominines are tested by using the *G*-test in $R \times C$ tests of independence (Sokal and Rohlf, 1995) with Williams's (1976) correction applied in all comparisons.

RESULTS

Degree and pattern of dimorphism in modern hominines

Most craniofacial measurements show statistically significant sex differences in the human and chimpanzee samples, the male face being consistently larger (Table 4; Fig. 4). Chimpanzees are on average slightly more sexually dimorphic than humans in these measurements. Both subspecies of gorilla show a much higher degree of sexual dimorphism. All variables show statistically significant sex differences in the lowland gorillas, while a few do not in the mountain gorilla sample. The ISDs for the mountain gorillas are also lower than for the lowland gorilla.

One aspect of pattern shared among modern hominines is that relatively low levels of craniofacial dimorphism are found in the alveolar arch and palate. This is clear from average values and from visual appraisal of Figure 4.

In addition, facial breadths and heights have on average similar levels of dimorphism in the hominine samples. The orbits are relatively less dimorphic than other areas in great apes, as is postorbital breadth, but in neither case do humans show the

TABLE 4. Craniofacial variation and sexual dimorphism in extant hominines¹

	Modern humans			Chimpanzees			Lowland gorillas			Mountain gorillas		
	CV (%)	ISD	t-test	CV (%)	ISD	t-test	CV (%)	ISD	t-test	CV (%)	ISD	t-test
Facial heights												
ORBH	6.9	3.4	*	6.1	0.7	—	8.1	9.7	***	5.4	2.2	—
GLAH	6.9	4.2	*	8.0	7.3	***	12.2	23.7	***	9.1	16.4	***
UPFH	7.3	7.0	***	8.5	7.8	***	12.6	24.7	***	9.3	17.0	***
NASH	7.1	9.0	***	9.0	9.9	***	12.8	25.4	***	7.3	9.8	**
OALH	9.3	5.7	*	8.0	9.8	***	13.9	26.7	***	9.4	18.3	***
OJUH	8.4	5.0	*	8.9	9.7	***	14.6	27.8	***	11.6	22.8	***
FORH	10.7	6.8	*	7.7	7.1	***	15.0	26.2	***	11.1	20.1	***
MALH	10.7	6.4	*	11.3	11.2	***	15.2	27.5	***	11.8	21.0	***
ALVH	11.4	2.6	—	15.1	2.0	—	17.8	20.4	**	16.4	28.8	***
Average	8.7	5.5		9.2	7.3		13.6	23.6		10.2	17.4	
Facial breadths												
ORBB	4.0	4.8	***	5.2	3.3	*	8.5	14.6	***	8.3	11.8	***
SUFB	3.9	4.8	***	6.3	8.2	***	10.2	20.4	***	9.0	17.3	***
ITOB	9.9	3.9	—	13.0	11.8	***	21.7	33.8	***	18.9	24.9	**
BMAB	5.4	5.6	***	5.5	5.4	***	9.5	16.0	***	8.3	14.4	***
ZYGB	4.4	6.3	***	6.9	11.0	***	11.1	21.9	***	8.9	18.5	***
IFOB	7.7	6.5	**	6.8	6.5	***	11.3	19.9	***	8.0	14.0	***
NASB	6.9	3.3	—	8.2	7.8	***	13.3	17.3	***	10.0	15.0	***
SNOB	—	—	—	6.3	6.7	***	10.2	18.7	***	10.9	18.7	***
Average	6.0	5.0		7.3	7.6		12.0	20.3		10.3	16.8	
Maxillo-alveolar and palatal												
ANMB	5.3	4.6	***	5.7	5.9	***	8.4	14.6	***	10.8	22.1	***
MAXB	4.9	2.7	*	4.6	1.8	—	6.8	11.3	***	7.0	10.3	***
APAB	6.5	4.7	**	7.4	1.3	—	11.0	15.3	***	11.0	17.3	***
PALB	7.2	4.6	*	8.0	4.6	*	10.7	17.3	***	9.5	4.9	—
MAXL	5.8	1.9	—	6.5	3.1	—	10.3	17.4	***	9.0	17.7	***
PMXL	4.9	1.8	—	5.0	1.8	—	6.1	8.1	***	6.5	10.4	***
Average	5.8	3.4		6.2	3.1		8.9	14.0		9.0	13.8	
Facial projections												
GLAP	5.7	6.1	***	5.7	6.6	***	10.0	19.2	***	10.2	18.6	***
PROP	5.8	5.8	***	6.3	6.2	***	11.9	24.0	***	11.8	25.0	***
ZYMP	6.4	4.8	**	7.3	9.6	***	12.3	24.6	***	12.1	25.9	***
MALP	6.1	5.2	**	6.7	7.7	***	12.2	24.6	***	12.9	26.8	***
Average	6.0	5.5		6.5	7.5		11.6	23.1		11.8	24.1	
Other												
POSB	4.5	3.4	**	4.7	1.3	—	5.5	6.2	**	5.0	−0.7	—
All	6.8	4.8		7.5	6.3		11.5	19.9		10.0	16.8	

¹ See Table 2 for measurement abbreviations. CV, Pooled-sex coefficients of variation. ISD = [(male mean/female mean) − 1] × 100.

* Significance level of a *t*-test of the difference between males and females: *P* < .05.

** Significance level of a *t*-test of the difference between males and females: *P* < .01.

*** Significance level of a *t*-test of the difference between males and females: *P* < .001.

same pattern. In humans, the measurement of postorbital breadth is more strongly correlated with overall facial size than it is in species with a constricted postorbital region.

A dramatic difference between mountain gorillas and other taxa is the elevated dimorphism in the various measures of facial projection from porion. The alveolar arch and palate are also more dimorphic in mountain gorillas when compared to other craniofacial measurements.

An inspection of the overall distribution of ISDs in extant hominines, as portrayed in Figure 4, shows that each group possesses a unique pattern of dimorphism. However, chimpanzees and lowland gorillas show very

similar patterns despite the strong difference in degree of dimorphism. Both are more different from modern humans than they are from each other. These similarities and differences among modern hominines are summarized by the rank correlation coefficients between ISDs for different species (Table 5). The relatively low correlations of the mountain gorilla ISDs with those for other species probably result in part from the small sample size available as well as differences pointed out above.

Size variation in early hominins

For the analysis of metrical variation, raw data for *A. africanus* are given in Table 6.

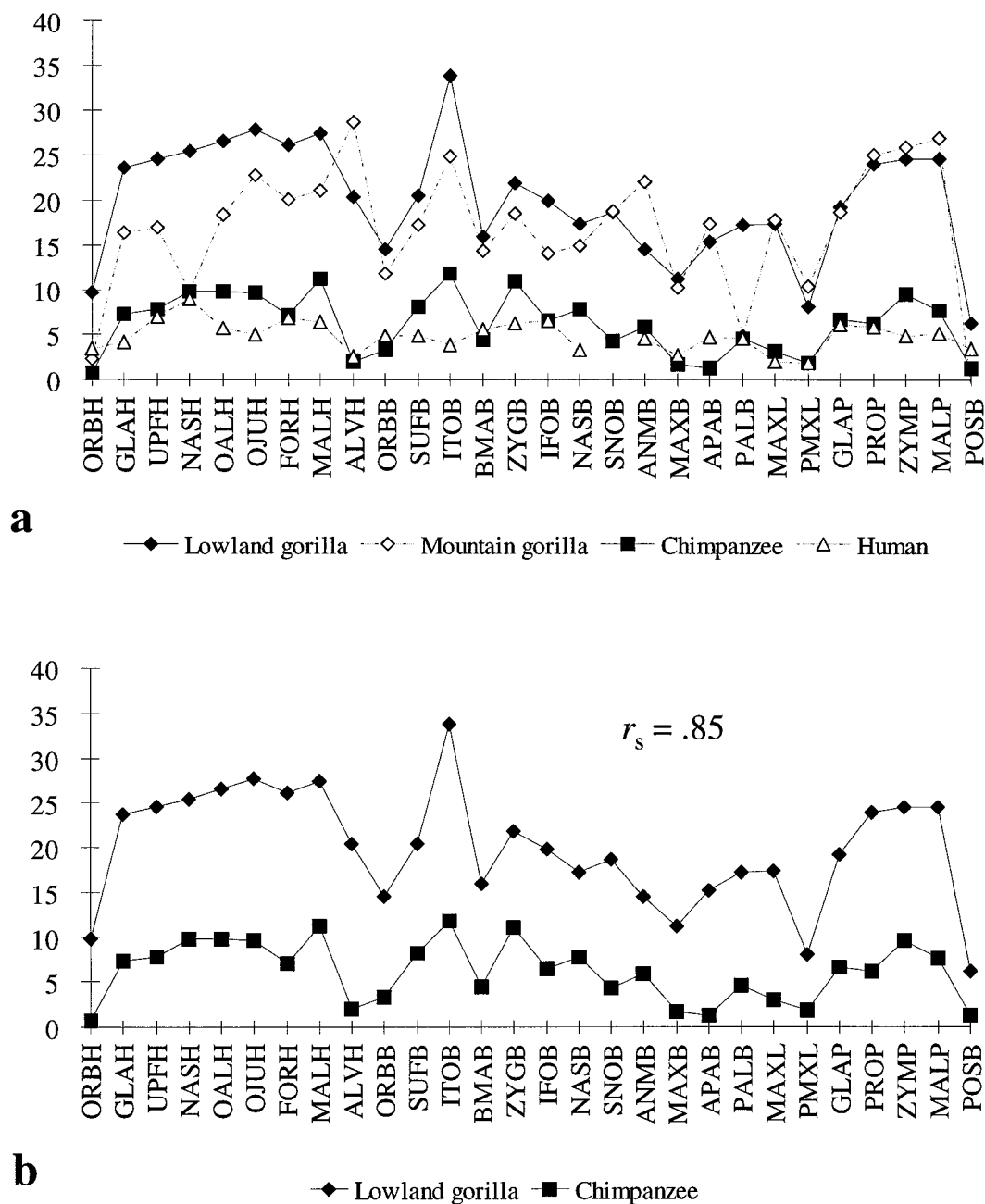


Fig. 4. Profiles of indices of sexual dimorphism in modern hominines. **a:** All hominine samples. **b:** Chimpanzees and lowland gorillas. The Spearman rank correlation between the profiles for chimpanzees and lowland gorillas is highly statistically significant ($P < .001$). Abbreviations are from Table 2.

The max/min ratios for specimens of *A. africanus* (Stw 505 and MLD 6 or Sts 17) as well as those for *A. boisei* (Table 7, OH 5 and KNM-ER 732) exceed the max/min ratio of

the entire sample of 63 chimpanzees—hence the probabilities of 0% in Table 8. Figure 5 demonstrates this graphically for *A. africanus*. The size range of *H. habilis* (Table 7)

TABLE 5. Interspecific rank correlations among indices of sexual dimorphism for all craniofacial dimensions¹

	Chimpanzees	Lowland gorillas	Mountain gorillas	Humans
Chimpanzees	1			
Lowland gorillas	0.85***	1		
Mountain gorillas	0.42**	0.60***	1	
Humans	0.56**	0.58**	0.18	1

¹ Spearman's rank correlation coefficient r_s .** $P < .01$.*** $P < .001$.

may be exceeded with extremely low probability (0.8–10.2%) from random samples of chimpanzees depending on what variables are used. The lowest frequency is found when the largest number of variables is used. Because these variables are more representative of the preserved crania, this result may more accurately represent the degree of size variation in *H. habilis*.

Whereas the size ranges of the pooled-site *A. africanus* sample and of *A. boisei* exceed that of 64 Zulu crania, the size ranges of Sterkfontein *A. africanus* and *H. habilis* may be sampled with low probabilities from the human sample (for Sterkfontein *A. africanus*, 3.3–15.3%). For both *A. africanus* and *H. habilis*, the lower probabilities are associated with more representative sets of variables.

Gorillas are the most highly dimorphic hominines and offer a much greater range of size from which to sample. The max/min ratio of *A. boisei* may be found in more than 20% of the random samples of gorillas. There is a dramatic difference between the frequencies associated with *A. boisei* on the one hand (21.9–25.8%) and *A. africanus* (84.2–96.8%) and *H. habilis* (75.7–87.6%) on the other, in that the size ranges in the latter two species are exceeded by random samples of gorillas in most instances. The probability levels for *A. boisei* are low but not low enough to indicate a convincing level of statistical significance.

These results have implications for the overall degree of sexual dimorphism even though it is not directly estimated. The probabilities associated with *A. africanus* and *H. habilis* suggest that the two species share a degree of sexual dimorphism in craniofacial size greater than that present in humans and chimpanzees but less than

that present in gorillas. The bootstrapping method takes into account the fact that although the absolute craniofacial size range in *A. africanus* is greater than in *H. habilis*, so is the sample size. In neither of these species is the range of size so excessive that it justifies a division of the samples into two species. Furthermore, there are few differences between the results for Sterkfontein *A. africanus* and those for the pooled-site sample.

In *A. boisei*, the degree of sexual dimorphism in the face is evidently very high. It is nonetheless probable that this degree is no greater than that found in gorillas, and therefore a conservative approach suggests that the variation can be accommodated in a single species.

Discrete estimates of sexual dimorphism in *A. africanus*

The results from the sex-assignment method of estimating dimorphism for *A. africanus* are summarized in Table 9 (see Table 6 for raw data). The result is approximately 11% whether Sts 5 is postulated to be a male or female. If both Sts 5 and Stw 13 are considered to be females, the estimate is 13.2%. In any case, the resulting values are somewhat larger than those for chimpanzees and humans and somewhat less than for gorillas. In this method, individual characters are much more variable in their index values of dimorphism than they are for the larger samples of extant hominines. Thus, depending on the sex determinations used, these values range from approximately 0% (no dimorphism) to 24–25%. They also vary depending on the sex assignment of crania. These differences should not be emphasized, because the sample is small, and for certain

TABLE 6. Craniofacial measurements in adults of *A. africanus*¹

	ORBH	GLAH	UPFH	NASH	OALH	OJUH	FORH	MALH	ALVH	ORBB	SUFB	ITOB	BMAB	ZYGB	IFOB	NASB	SNOB	ANMB	MAXB	APAB	PALB	MAXL	PMXL	POSB
MLD 6					43.0	43.9	32.0					(15.0)			(40.0)	(22.0)	(41.0)	(45.4)		(32.0)				39.9
MLD 9									23.0							(27.0)	(51.0)	(48.0)		(30.0)	(38.0)			41.6
TM 1511					52.0	55.5	35.3	28.2	29.0	36.0			(103.0)		(49.0)	(24.0)	(49.0)	(47.0)		(35.0)		54.0		41.2
TM 1512						50.1	35.4		25.5						(40.0)	(22.0)	(44.0)							
Sts 5	30.5	75.3	70.0	47.6	49.0	57.8	38.0	25.1	30.0	35.2	95.1	15.5	105.0	126.7	43.6	27.0	45.6	45.4	65.4	33.0	36.4	50.4	42.0	66.7
Sts 17		72.0			43.0	46.0	31.5	20.0	21.1		(92.0)		(92.0)		(45.0)	26.1	47.0	43.5	60.0	32.0	36.0	50.0	40.0	(76.0)
Sts 53									22.0							24.0	44.1	45.6	63.8	31.4	31.2	47.0	37.7	
Sts 63	31.2					55.0																		
Sts 71	31.0	77.0	70.2	50.9	47.9	51.3	37.8	26.0	23.0	35.1	(88.0)	16.1	(97.0)	(124.0)	(45.0)	27.0	(48.0)	46.6	72.0	35.2	40.0	52.0	43.4	(66.0)
Sts 3009									25.0								(43.0)		(28.0)			52.0	39.5	
Stw 13	31.1	88.0	80.0	54.0	51.0	62.0	37.0	28.0	29.0			15.0	(100.0)		(38.0)	23.6	42.0	68.0	34.0	35.0	53.0	45.3		
Stw 73									26.6							22.0	46.0	43.0	60.0	30.0	29.0	53.0	41.7	
Stw 505	37.2	98.0	91.0	64.0	58.0	63.0	40.0	31.3	29.0		(107.0)	18.6	(108.0)		(58.0)	29.5	59.0	55.0		37.0				(71.0)

¹ Measurements are in millimeters. Abbreviations are as in Table 2. Values in italics are estimates. Values in parentheses are doubled from a measurement to the midline.

TABLE 7. Craniofacial measurements used in analysis of size variation in *A. boisei* and *H. habilis*¹

	ORBH	GLAH	NASH	OALH	OJUH	FORH	MALH	ALVH	ORBB	SUFB	ITOB	BMAB	IFOB	NASB	ANMB	MAXB	APAB	PMXL	GLAP	PROP	ZYMP	MALP	POSB
<i>A. boisei</i>																							
OH 5 ²	33.4	112.1	70.2	75.1	79.6	46.0	38.5	42.2	40.0	115.4	23.4	121.5	60.5	31.8	48.2	81.8	36.3	53.4	107.0	146.0	107.2	123.2	68.1
ER 732 ³	30.0		48.0	46.0	51.7	31.8	29.0		36.0	90.0	17.0	100.0	48.0	28.0		62.0		43.7	88.0	105.0	83.0	104.8	65.0
<i>H. habilis</i>																							
ER 1470 ³	35.0	96.0	57.0	58.0	63.0	37.0	35.0	31.0	39.5	114.0	23.0	113.0	52.0	27.0	54.0	80.0	38.0	45.0	100.0	123.0	92.5	108.5	81.0
ER 1813 ³	30.0	69.4	42.0	44.1	46.7	32.3	27.0	25.0	33.0	100.0	20.0	90.0	47.0	23.0	43.6	65.0	29.8	38.0	87.0	111.0	74.0	85.0	70.0

¹ Measurement abbreviations are as in Table 2. Measurements taken on casts except where noted.

² Values in italics taken from Tobias (1967).

³ Values in italics taken from Wood (1991).

TABLE 8. Probabilities (%) of obtaining from extant hominine samples max/min size ratios greater than those that characterize early hominin species¹

	Comparison	Variable set	Size ratio	n	Humans	Chimpanzees	Gorillas
<i>A. africanus</i>	Stw 505/MLD 6	8a	1.299	15	0.0**	0.0**	96.8
	Stw 505/Sts 17	8b	1.287	12	15.3	0.0**	85.4
	Stw 505/Sts 17	12	1.284	12	3.3*	0.0**	84.2
<i>H. habilis</i>	KNM-ER 1470/1813	8a	1.216	6	9.0	8.7	87.6
		8b	1.220		14.3	10.2	84.6
		12	1.241		6.8	3.0*	75.7
		19	1.209		0.5**	0.8*	81.0
<i>A. boisei</i>	OH 5/KNM-ER 732	8b	1.346	6	0.0**	0.0**	25.8
		19	1.284		0.0**	0.0**	21.9

¹ Based on 1,000 random samples of each extant species. All probabilities (%) are reported for comparisons of geometric means and have an estimated error of $\pm 2\%$. See Table 3 for definition of variable sets. The chimpanzee and gorilla samples contain multiple subspecies.

* $P < .05$.

** $P < .01$.

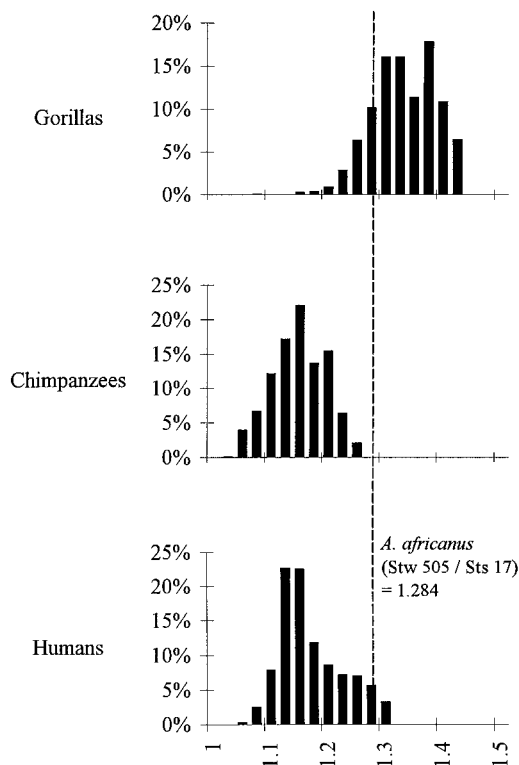


Fig. 5. Frequency histograms of max/min ratios of 1,000 random samples of extant hominine geometric means. The 12 variable set is defined as those measurements available on both Stw 505 and Sts 17 (see Table 3). Sample size is $n = 12$.

variables changing the assignment of a single cranium has a pronounced effect. Average levels of variation, on the other hand, are relatively stable.

TABLE 9. Discrete estimates of indices of sexual dimorphism for *A. africanus*¹

	Sex assignments ²		
	A	B	C
ORBH	11.1	6.2	20.5
GLAH	24.6	17.1	25.6
OALH	17.6	18.0	17.8
OJUH	20.8	24.6	14.3
FORH	7.5	10.0	6.7
MALH	23.1	22.4	20.1
ALVH	12.6	21.7	7.1
ITOB	8.6	5.9	21.2
BMAB	11.2	6.5	7.7
IFOB	13.6	11.4	28.2
NASB	5.9	8.5	10.1
SNOB	11.9	10.1	18.8
ANMB	8.7	7.1	9.7
MAXB	3.3	1.7	— ³
APAB	4.1	3.6	3.4
PALB	2.3	2.7	7.2
MAXL	7.4	5.9	7.3
PMXL	5.7	6.0	-1.4
Average	11.1	10.5	13.2

¹ Measurement abbreviations are as in Table 2. Index = [(male/female) \times 100] - 100.

² Sex assignments are as follows: A: males—MLD 9, TM 1511, Sts 5, Stw 13, Stw 505; females—MLD 6, TM 1512, Sts 17, Sts 53, Sts 71; B: males—MLD 9, TM 1511, Stw 13, Stw 505; females—MLD 6, TM 1512, Sts 5, Sts 17, Sts 53, Sts 71; C: males—MLD 9, TM 1511, Stw 505; females—MLD 6, TM 1512, Sts 5, Sts 17, Sts 53, Sts 71, Stw 13.

³ Values not available for males. Because this is usually a low dimorphism measurement but is missing, the average value (13.2%) for these sex assignments is slightly inflated relative to the other assignments.

The other technique to estimate the degree of sexual dimorphism in *A. africanus* uses the coefficient of variation. CVs for measurements of the face in *A. africanus* are given in Table 10 and are moderately high. Those for the alveolar arch and palate are on average lower than those for other facial measurements.

TABLE 10. Variation in the adult faces of *A. africanus*¹

	Mean	n	Sample range	SD	CV	SE of CV
Facial heights						
ORBH	32.2	5	30.5–37.2	2.8	9.2	3.4
GLAH	82.1	5	72.0–98.0	10.7	13.7	5.2
UPFH	77.8	4	70.0–91.0	10.0	13.6	6.0
NASH	54.1	4	47.6–64.0	7.1	13.9	6.1
OALH	49.1	7	43.0–58.0	5.3	11.1	3.4
OJUH	53.8	9	43.9–63.0	6.6	12.6	3.3
FORH	35.9	8	31.5–40.0	3.0	8.5	2.4
MALH	26.4	6	20.0–31.3	3.8	15.0	5.0
ALVH	25.7	11	21.1–30.0	3.2	12.7	2.9
Average					12.3	
Facial breadths						
ORBB	35.4	3	35.1–36.0			
SUFB	95.5	4	88.0–107.0	8.2	9.1	4.0
ITOB	16.0	5	15.0–18.6	1.5	9.8	3.7
BMAB	99.7	6	85.0–108.0	8.1	8.5	2.8
ZYGB	125.4	2	124.0–126.7			
IFOB	44.8	8	38.0–58.0	6.4	14.7	4.1
NASB	24.9	11	22.0–29.5	2.5	10.5	2.4
SNOB	47.0	11	41.0–59.0	5.0	10.8	2.5
Average					10.6	
Maxillo-alveolar and palatal						
ANMB	46.3	11	43.0–55.0	3.3	7.4	1.7
MAXB	64.9	6	60.0–72.0	4.7	7.5	2.5
APAB	32.5	11	28.0–37.0	2.6	8.3	1.9
PALB	35.1	7	29.0–40.0	3.8	11.3	3.4
MAXL	51.4	8	47.0–54.0	2.2	4.5	1.2
PMXL	41.2	10	37.7–45.3	2.1	5.3	1.3
Average					7.4	
Other						
POSB	69.9	4	66.0–76.0	4.6	7.0	3.1
Average CV of 18 italicized measurements					10.1	0.7

¹ Measurement abbreviations as in Table 2. CVs and their standard errors (SE) are calculated using the small-sample adjustment (Sokal and Braumann, 1980).

The average CV for 18 dimensions of the face in *A. africanus* is 10.08%. The corresponding average CVs in the modern hominines for this subset of craniofacial measurements are as follows: chimpanzees, 7.99%; lowland gorillas, 12.1%; mountain gorillas, 10.5%; humans, 7.58%. The average values for indices of sexual dimorphism are as follows: chimpanzees, 5.75%; lowland gorillas, 20.1%; mountain gorillas, 16.4%; humans, 4.34%. The correlation between the average CVs and the average ISDs is $r = 0.994$, as shown graphically in Figure 6. A reduced major axis regression line yields an estimated ISD of 13.2% for *A. africanus*, an estimate which is most similar to that determined above (13.2%) when Sts 5 and Stw 13 are considered as females. This result is therefore consistent with MLD 9, TM 1511, and Stw 505 being the only males, but it does not represent proof of such.

Facial morphology in modern hominines and *A. africanus*

Supraorbital region. Sex differences in the prominence of the superciliary eminence are statistically significant in Zulu crania (Table 11) ($G = 22.65$, $P < .001$), a result similar to that of De Villiers (1968). The supraorbital torus of the chimpanzee is most frequently thicker medially than laterally, and in some cases (21% of males, 27% of females) the medial portion of the supraorbital torus is relatively distinct. It is doubtful that this distinct thickening is structurally homologous to the anteriorly prominent superciliary eminence in humans. A few female gorillas show a similar morphology, but in most females and nearly all male gorillas, the supraorbital tori are usually of relatively even, robust thickness across the supraorbital region. The measurement of vertical thickness of the supraorbital torus at the highest point on the superior orbital margin reveals significant sex differences in both chimpanzees and gorillas, though a few outliers occur in both sexes (Table 12).

In *A. africanus*, the supraorbital arch is clearly divided into distinct superciliary and supraorbital components in TM 1511, Sts 5, and Stw 505. The superciliary eminence is more strongly developed in Stw 505 than the other specimens. The eminence in Sts 5 protrudes somewhat superiorly, forming a slight ridge over the medial portion of the orbit (preserved on the right but abraded on the left). A division of the supraorbital arch can be detected in Sts 63, Sts 71, and Stw 13, but these specimens do not have prominent superciliary eminences.

Values of supraorbital arch thickness in *A. africanus* convey an absolute size and range similar to that of the chimpanzee, though the CV is high. Both chimpanzees and gorillas are very dimorphic in the supraorbital arch. In *A. africanus*, arch thickness is only somewhat related to overall facial size, as Sts 17 has a very thick arch, but that of Stw 13 is thin. Measured at the highest point of the arch, the vertical thickness for Stw 505 is similar to those of Sts 5 and Sts 17, but it should be noted that this dimension becomes substantially greater medially in Stw

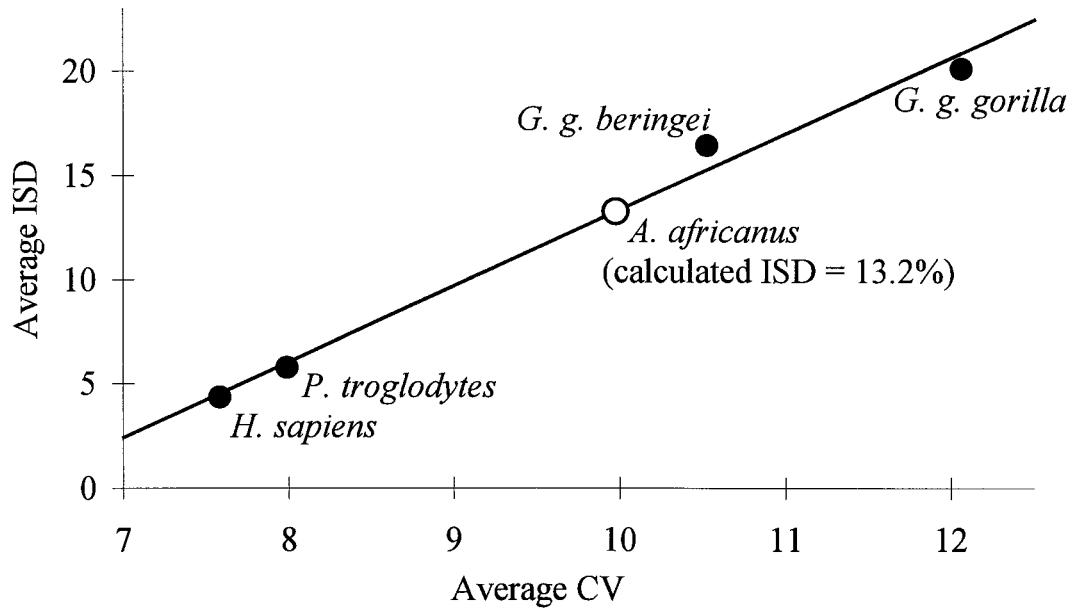


Fig. 6. Estimation of the degree of sexual dimorphism in *A. africanus* using the CV-based method. See text for explanation. The equation of the regression line is $ISD = (3.64 \times CV) - 23.1$; $r = .994$.

TABLE 11. Prominence of the superciliary eminence in the modern human sample

	Males		Females	
	n	%	n	%
Absent	6	19	19	59
Slight	15	47	13	41
Moderate	7	22	0	0
Marked	4	13	0	0
Total	32		32	

505. Although there is not a clear relationship to facial size, the overall level of variation may imply high dimorphism.

Glabella. The anterior prominence of glabella is sexually dimorphic in humans ($G = 24.6$, $P < .001$) and chimpanzees ($G = 7.90$, $P < .05$) (Table 13). This dimorphism is more striking in the human sample, where nearly all specimens falling in the moderate or marked categories are male. In addition, a midline depression occurs in four of the five males with marked projection of the glabellar region, four of the 14 males with moderate projection of the glabellar region, and two of the 11 males with slight projection of the glabellar region. The total frequency of

the midline depression is 31% in the male sample, and it is fairly clear from its distribution that it is related to glabellar prominence. This correlation owes itself to the effect of the superciliary eminences, which often constitute the most anterior contour of the frontal bone on either side of midline in those specimens with the most prominent glabellar regions. Four (13%) female crania possess a midline depression in the glabellar region; three of these have slight glabellar prominence.

Specimens of both sexes of chimpanzee fall at the extremes of glabellar prominence, but males usually have greater development of this character. The most common pattern observed in the female chimpanzee is flat. In rare cases (8% of males, 13% of females), a very shallow midline depression of glabella is discernible in chimpanzee crania.

When gorilla subspecies are pooled, the modal categories for both sexes are slight prominence. Thus, the bulk of the sample possesses a glabellar region of flat to moderate prominence, but two mountain gorilla females (8%) have receding glabellar regions. The small sample of mountain goril-

TABLE 12. Vertical thickness of the supraorbital arch in extant African apes and *A. africanus*¹

	Mean	n	Sample range	SD	CV (%)	ISD ²
<i>P. troglodytes</i> (mixed subspecies)						
M + F	8.5	57	5.2–11.8	1.58	18.7	20.8
M	9.3	28	6.8–11.8	1.54	16.7	
F	7.7	29	5.2–10.5	1.19	15.6	
<i>G. gorilla</i> (mixed subspecies)						
M + F	12.8	52	7.3–17.6	2.36	18.4	
<i>G. g. gorilla</i>						
M + F	13.0	33	7.3–17.5	2.47	19.1	24.6
M	14.5	16	11.8–17.5	1.97	13.8	
F	11.6	17	7.3–17.1	2.08	18.2	
<i>G. g. beringei</i>						
M + F	12.6	19	9.3–17.6	2.18	17.6	26.2
M	13.9	10	11.7–17.6	2.13	15.6	
F	11.0	9	9.3–11.7	0.84	7.8	
<i>A. africanus</i>						
M + F	8.0	5	6.0–10.0	2.00	26.1	
Sts 5	9.4					
Sts 17	8.9					
Sts 71	5.8					
Stw 13	6.0					
Stw 505	10.1					

¹ Measured at the highest point on the superior orbital margin.² All sex differences in extant apes are statistically significant at the $P < .001$ level.TABLE 13. Anterior prominence of glabella in hominines¹

	Receding	Flat	Slight	Moderate	Marked
<i>H. sapiens</i>					
Males		2 (6)	11 (34)	14 (44)	5 (16)
Females		11 (34)	19 (59)	2 (6)	
<i>P. troglodytes</i>					
Males	3 (10)	7 (24)	17 (59)	2 (7)	
Females	3 (10)	18 (60)	8 (27)	1 (3)	
<i>G. g. gorilla</i>					
Males		5 (25)	9 (45)	4 (20)	2 (10)
Females		3 (17)	11 (61)	3 (17)	1 (6)
<i>G. g. beringei</i>					
Males		3 (23)	5 (39)	4 (31)	1 (8)
Females	2 (25)	2 (25)	3 (38)	1 (12)	
<i>A. africanus</i>			Sts 71 TM 1511	Sts 17	Sts 5 Stw 13 Stw 505

¹ Italics indicate an estimate on a fragmentary specimen. Values in parentheses are percentages of the samples.

las shows a perceptible difference between males and females, but, because the sample is so small, the difference is not statistically significant. The prominence of glabella is of similar degree in both sexes of both subspecies.

In the pooled-subspecies sample, only one female lowland gorilla cranium possesses a slight midline depression of glabella. The absence of this feature is presumably related to the lack of superciliary eminences in gorillas.

In *A. africanus* (Table 13), the glabellar mound is most prominent in Sts 5, Stw 13,

and Stw 505, giving the impression of "being undercut by a marked infraglabellar or supranasal notch" (Clarke, 1977:74). The morphology differs among these three, as the glabella projects as a single, pointed mound of bone in Sts 5 and Stw 13 but is a broad structure with a midline depression in Stw 505.

TM 1511 and Sts 71 have slightly prominent glabellar regions. TM 1511 has a midline depression similar to that of Stw 505. As discussed above, the midline depression is related to the development of superciliary eminences that do not join across the mid-

line. In specimens that lack the depression, such as Sts 5, the superciliary eminences do not contribute to the prominence of glabella.

Projection and hollowing of the central face. The human face contrasts with those of other hominines in that nasal prominence is often pronounced and, relative to this prominence, the zygomatic process projects only weakly anteriorly. Variation in nasal prominence is caused by a number of features of the nasal bones themselves: their shape, their anterior projection, and the angle between them (De Villiers, 1968; Clarke, 1977; Franciscus and Trinkaus, 1988; Tobias, 1991). De Villiers pointed out that the sexual dimorphism in each of these factors is insignificant.

A central facial hollow is not present in *Pan*, yet there is variation in the combination of features which leads to the expression of such a feature in some *Australopithecus*. In *Pan*, although the nasal bones themselves are usually flat transversely, they are the most anterior part of the face at that level because of the gradual anterior slope of the maxillary frontal processes as they approach the nasomaxillary suture. The degree of central facial projection does vary, and in about one-quarter of the sample examined here the maxillae were noted to be nearly flat transversely in the area of their frontal processes. On no specimen does the zygomatic arch project anteriorly far enough to obscure the nasal region as seen in lateral view. No sexual dimorphism in any of these features is evident.

The area of the nasal bones is more prominent on the mountain gorilla face than on that of the lowland gorilla. The nasal bones are positioned on frontal processes of the maxilla that face laterally to variable degrees. In some specimens there is a distinct mediolateral step on the maxillary frontal processes. In lowland gorillas, on the other hand, the nasal bones are usually set in a maxilla that is nearly flattened in a coronal plane (cf. Hofer, 1972; Franciscus and Trinkaus, 1988). Less often they resemble mountain gorillas. In two male lowland gorillas in this sample, the nasal bones are set just behind the anterior projection of the

zygomatic bones in lateral view. Thus, central facial hollowing is apparently a rare trait in male lowland gorillas and not present in any of the females.

The degree of central facial hollowing is variable within the *A. africanus* sample. Nasal bones themselves are not prominent in any specimen, but when the maxillary frontal processes face somewhat laterally, the nasal bones form the profile of the face from lateral view. In Sts 5, Sts 17, Sts 52, and probably Stw 13 (here the nasal region has been crushed posteriorly), this is the case. TM 1511 and TM 1512 lack the relevant area of the central face, but what is preserved of the maxillary frontal processes suggests slight central facial prominence.

Stw 505 has essentially a flat central face, while the area is slightly hollowed in Sts 71 and probably MLD 6. The nasal bones and the frontal processes of the maxilla in MLD 6 are well-preserved and anteriorly concave. The medial portion of the zygomatic process is present above the infraorbital foramen on the right side and projects laterally in a coronal plane. Its anterior prominence further laterally is not preserved, but the overall shape of the preserved area is that of a slight central facial hollow. Sts 71 is the only specimen from Sterkfontein in which the anterior contour of the prominent zygomatic clearly forms the profile of the central face from lateral view.

Concavity of the infraorbital region (Table 14). The infraorbital region is usually of slight to moderate concavity in *Zulus*; only a few specimens possess either a flat or markedly concave surface. Except for the few specimens with flat infraorbital regions, the determination of infraorbital concavity in humans is an estimation of the depth of the hollowed area (canine fossa) below the infraorbital foramen on the anterior surface of the body of the maxilla. Sex differences in the excavation of the infraorbital region are found here and by De Villiers (1968) to be insignificant.

On the other hand, sex differences are statistically significant ($G = 14.4$, $P < .005$) in the chimpanzee. Because the concavity, or excavation, of the infraorbital region is

TABLE 14. *Infraorbital concavity in hominines*¹

	Flat	Slight	Moderate	Marked
<i>H. sapiens</i>				
Males	1 (3)	14 (44)	13 (41)	4 (12)
Females	1 (3)	15 (47)	13 (41)	3 (9)
<i>P. troglodytes</i>				
Males		16 (55)	11 (38)	2 (7)
Females	7 (23)	19 (63)	4 (13)	
<i>G. g. gorilla</i>				
Males		11 (55)	6 (30)	3 (15)
Females	5 (28)	8 (44)	3 (17)	2 (11)
<i>G. g. beringei</i>				
Males		3 (21)	11 (79)	
Females		4 (50)	3 (38)	1 (12)
<i>A. africanus</i>		MLD 45	Sts 5	
		TM 1511	Stw 13	
		TM 1512		
		Sts 17		
		Sts 52 ²		
		Sts 71		
		Stw 505		

¹ Values in parentheses are percentages of the samples.² Immature specimen.

closely related to the degree to which a canine fossa is present, the canine dimorphism of chimpanzees lends the males somewhat greater concavity of the infraorbital region as a whole. Both males and females most often possess a slight hollowing of the infraorbital region, but the sexes differ in the next most common pattern. Many of the males have moderately or markedly concave infraorbital regions, while relatively few females do. The region is flat in a number of females but no males.

The infraorbital concavity in male lowland gorillas is slightly greater on average than in females. The primary difference between these distributions is that the infraorbital region in the female but not the male sometimes has the appearance of being flat. Most of the remainder in each sex show only slight hollowing of the region, and this similarity contributes to statistically insignificant sexual dimorphism, though the test produces a probability level close to 0.05 ($G = 5.28$, $G_{crit} = 5.99$).

The infraorbital region of the mountain gorilla is more excavated than that of the lowland gorilla, as expressed in the higher proportion of specimens with moderate infraorbital excavation. Most males have moderately concave infraorbital regions, while females are divided between the categories of slight and moderate excavation. With pooled

sexes, the differences in infraorbital excavation between the mountain and the lowland gorilla are statistically significant ($G = 11.5$, $P < .01$). In other words, the resulting pattern of infraorbital hollowing in gorillas follows a gradient from flat to slight excavation in female lowland gorillas to slight to moderate excavation in male lowland gorillas and probably female mountain gorillas to usually moderate excavation in male mountain gorillas.

The sample of *A. africanus* specimens is relatively limited in the variation of infraorbital concavity (Table 14). The infraorbital regions of eight of ten specimens are slightly concave, whereas those of Sts 5 and Stw 13 are moderately concave. When applied to *A. africanus*, these terms essentially convey variation in the topographic shift between the surface of the anterior pillar and the zygoma. None of these specimens exhibit a hollowed infraorbital region as is found in some extant hominines. Along the same lines, when a canine fossa is present, as in Sts 52, it is relatively confined and does not influence the overall topography of the infraorbital region. This also contrasts with the form in modern hominines, where the canine fossa usually refers to a broad area that encompasses much of the infraorbital region.

Anterior limit of the zygomatic process (Table 15). Sex differences in the position of the zygomatic process are not statistically significant in the modern hominine groups considered here. In each group, variation spans one or one-and-a-half tooth positions. The modal categories are the M1 for Zulus and mountain gorillas and the interalveolar septum between P4 and M1 for chimpanzees and lowland gorillas.

At the two extremes in *A. africanus*, the zygomatic process of Sts 5 has its anterior origin above the posterior half of the first molar alveolus, while those of MLD 6 and Sts 52 have theirs between the third and fourth premolars. In most of the *A. africanus* specimens, the anterior root of the zygomatic process is over P⁴ or P⁴/M¹.

TABLE 15. Anterior limit of the zygomatic process in hominines¹

	P ³ /P ⁴	P ⁴	P ⁴ /M ¹	M ¹	M ¹ /M ²
<i>H. sapiens</i>					
Males			12 (38)	17 (53)	3 (9)
Females		1 (3)	11 (36)	15 (48)	4 (13)
<i>P. troglodytes</i>					
Males		9 (32)	18 (64)	1 (4)	
Females		10 (34)	16 (55)	3 (10)	
<i>G. g. gorilla</i>					
Males		2 (10)	12 (60)	6 (30)	
Females		4 (22)	12 (67)	2 (11)	
<i>G. g. beringei</i>					
Males				12 (86)	2 (14)
Females			3 (38)	5 (62)	
<i>A. africanus</i>	MLD 6	MLD 9	TM 1511	Sts 5	
	Sts 52 ²	MLD 45	TM 1512		
		Sts 17	TM 1514		
		Sts 53	Sts 63		
		Sts 71	Sts 3009		
		Stw 391	Stw 13		
		Stw 505	Stw 498 ²		

¹ Values in parentheses are percentages of the samples.² Immature specimen.

The anterior pillar. Rarely do modern hominines express a structure resembling what Rak (1983) referred to as an anterior pillar in *A. africanus* and *A. robustus*, though the canine buttress of apes varies substantially in form. Rak hypothesized sexual dimorphism in the form of the anterior pillar in *A. africanus*.

The anterior pillar is absent in TM 1512, Sts 52, Stw 391, and Stw 498. Instead, a weak crest travels from the canine (TM 1512, Stw 391) or premolar (Stw 498) jugum to terminate low on the maxilla before reaching the infraorbital foramen. The crest does not diverge laterally. The canine jugum is separate from that of the third premolar and terminates at about the level of the subnasal margin. Above this, the bony surface faces more laterally than in specimens that do have an anterior pillar. The lateral border of the nasal aperture is less rounded than in other specimens.

Sts 52 is somewhat different from TM 1512, Stw 391, and Stw 498; its maxilla is more heavily buttressed, but the buttressing does not encompass the nasal margin. The canine and the premolar juga are not distinct entities, and a transverse buttress similar to that present in apes passes superior to the deep canine fossa. Sts 52 is an adolescent, and the ontogenetic ages of Stw

391 and Stw 498 are unclear. Among specimens lacking an anterior pillar, the only specimen that certainly represents a mature individual is TM 1512.

The anterior pillar is present in ten adults, and in all of these the canine and premolar juga are not distinct from one another. In other respects, the form of the pillar varies. In TM 1511, Sts 71, Stw 505, MLD 45, and probably MLD 9, the pillar is wide and weakly distinguished from the rest of the infraorbital region. The lateral contour of the pillar is directed laterally below the infraorbital foramen, developing into a slight crest in Sts 71. The lateral nasal margin is rounded except in Stw 505, where it is sharper.

The anterior pillar is narrow and markedly prominent in TM 1514, Sts 5, Sts 17, Stw 13, MLD 6, and probably Sts 63. It corresponds closely to Rak's (1983) definition, being clearly defined laterally by a maxillary furrow that terminates superiorly in the infraorbital foramen.

DISCUSSION

Modern hominines

Quantitative comparisons of extant hominines emphasize an important point about the degree and pattern of craniofacial sexual dimorphism: similarity in one does not imply similarity in the other. Chimpanzees and lowland gorillas are similar in pattern of dimorphism but not in degree. The human face is characterized by a novel pattern of sexual dimorphism among extant hominines, though the average degree of dimorphism differs little between humans and chimpanzees. In addition, mountain gorillas appear to be distinct in their pattern of craniofacial variation (as they are in dental dimorphism [Uchida 1992, 1998]), but this may be due in part to random error in their small-sample indices of sexual dimorphism.

A similarity in pattern among lowland gorillas and chimpanzees is not unexpected; Shea's (1983, 1985, 1988) work has suggested that "pygmy chimpanzees, common chimpanzees, and gorillas form a single ontogenetic and interspecific trajectory of size/shape change for many proportion compari-

sons" (Shea, 1983:278). A like profile of sexual dimorphism between chimpanzees and gorillas is a corollary of this ontogenetic scaling. It is also true that qualitative and quantitative differences exist between chimpanzees and lowland gorillas (O'Higgins et al., 1990; Wood et al., 1991; O'Higgins and Dryden, 1993). However, similarity in this case can be expressed in a relative sense, and in craniofacial variation the patterns in lowland gorillas and chimpanzees are more similar to one another than they are to other groups.

On the other hand, Wood et al. (1991) inferred that chimpanzees and modern humans share a common pattern of cranial and mandibular sexual dimorphism different from that of gorillas and orangutans. The basis for this statement was an appraisal of indices of sexual dimorphism like those used here (see Figs. 2 and 3 in Wood et al., 1991), but multivariate comparisons in the same paper supported a different conclusion: that all of the great apes share a basic similarity in cranial dimorphism. In any case, because my results focus on the face, where chimpanzees and gorillas are both influenced by strong canine dimorphism, a correspondence between their patterns is very clear.

Size variation in *A. africanus* and other hominins

With respect to *A. africanus*, the degree of craniofacial size variation was almost certainly intermediate between less dimorphic and more highly dimorphic modern hominines. It is improbable that the size range of *A. africanus*, as represented in the face, could be sampled from populations of humans or chimpanzees, but the same size range occurs in random samples of gorillas a majority of the time. Evidence of moderately high dimorphism in *A. africanus* makes the main assumption of a discrete estimate—that size is helpful in distinguishing males from females—more acceptable. These estimates indicate degrees of sexual dimorphism (10.5–13.2%) consistent with inferences from the resampling analysis of size variation.

The CV-based method of estimating sexual dimorphism does not require assigning sex to individual specimens and makes a mini-

mum of assumptions about the distribution of size in the sample. However, it is limited here by the few taxa available as reference groups. There are also two potential sources of conflicting systematic error. Plavcan (1994) has demonstrated that the CVs of pooled-sex samples can overestimate the level of sexual dimorphism in a sample where intrasexual variation is high. This may be expected to be the case with a fossil sample accumulated over a long period of time. On the other hand, the *A. africanus* size range might not be representative of the species being sampled as a result of a taphonomic predator selection bias towards smaller hominin individuals. It is unknown whether a cranium as large as Stw 505 was rare in the population or only rare in the sample. The possibility of these biases must be acknowledged, but they cannot be evaluated as yet. The CV-based estimate (13.2%) corroborates the other lines of inference, and this agreement is encouraging.

Examination of other fossil hominin taxa indicates that the degree of sexual dimorphism in the *A. africanus* face is not exceptional. *A. boisei* is somewhat more sexually dimorphic than *A. africanus* and bears more similarity to gorillas (cf. Wood, 1991). If the remains attributable to *H. habilis* represent one species, this species shares with *A. africanus* a moderately high level of sexual dimorphism.

To the extent that sexual dimorphism in mandibular size can be compared to sexual dimorphism in the upper face, a recent study using similar methodology to this one suggests that *A. afarensis* shows a degree of sexual dimorphism in the mandible that approaches that of gorillas, orangutans, and, it may be inferred, *A. boisei* (Lockwood et al., 1996). The dramatic differences in facial size between Hadar specimens such as A.L. 444–2 and A.L. 417–1, although not yet quantified, further testify to the high degree of sexual dimorphism in the skull of *A. afarensis* (Kimbel et al., 1994).

The finding that the degree of dimorphism in the *A. africanus* face is somewhat greater than in chimpanzees and humans but less than that found in gorillas recalls conclusions that *A. africanus* is strongly sexually

dimorphic in body size (Wolpoff, 1975; McHenry, 1976; Tobias, 1980). On the other hand, work by McHenry (1992) estimates the levels of body size sexual dimorphism in *A. africanus*, *A. boisei*, and *H. habilis* to be lower than my estimates for facial size dimorphism (accounting for differences in dimensionality). This consistent difference may represent a methodological difference, a sampling phenomenon, or an indication that sexual dimorphism in the face can be more pronounced in some early hominins than sexual dimorphism in body size. Recent work by Plavcan (1998) suggests that the latter may be the case.

A discussion of size-based sexual dimorphism is also relevant to taxonomy. The results presented here demonstrate that there is little evidence for excessive variation in craniofacial size in several early hominin species if moderate to high degrees of sexual dimorphism are accepted. For early *Homo*, which has received the most attention in this regard, these results are essentially consistent with the size comparisons of Kramer et al. (1995) and Grine et al. (1996) and in contrast to those of Lieberman et al. (1988). These three studies were all based in part on pairwise comparisons (Kramer et al. [1995] used both pairwise and sample comparisons). Differences among them reflect the comparative samples and variables used.

The results of this study are more conservative than any previous analysis of craniofacial size variation in early *Homo*, as they suggest a very high probability (75–90%) of sampling equivalent variation in gorillas. High probabilities result because of the bootstrapping methodology. Pairwise comparisons of any kind produce lower probability estimates than bootstrapping with sample sizes greater than two. When interpreting relatively extreme specimens in a sample, pairwise comparisons can lead to erroneous conclusions (Lockwood et al., 1996). The differences between KNM-ER 1470 and KNM-ER 1813 or, for *A. africanus*, Stw 505 and Sts 17 must be considered in light of the entire samples available. Bootstrapping, unlike pairwise comparisons, is directed to the question of sample variation and is there-

fore a more appropriate method for comparing fossil samples to modern populations.

The point has also been raised that highly dimorphic hominines, such as gorillas, are not appropriate analogues for variation in early hominins (Kramer et al., 1995; Grine et al., 1996). For craniofacial shape variation, the present study supports that view, as canine dimorphism in great apes has an impact on facial morphology not to be found in *A. africanus* or other fossil hominins.

However, size and shape should probably be considered separately in choosing appropriate reference populations, because gorillas do appear to set appropriate bounds for size variation in early hominins. To assert that they do not would presuppose the conclusion that early hominins were not very size-dimorphic. Thus, a consistent application of size standards such as these would result in recognizing the size morphs of *A. boisei*, *A. afarensis*, and probably *A. africanus* as different species. Among *Australopithecus* species, only *A. robustus* shows no evidence of significant size variation. The recognition that early hominins can show moderate to high levels of size dimorphism does not discount the morphological shape differences between, for example, specimens considered to be *H. rudolfensis* and other specimens of early *Homo*. On the contrary, it suggests that these differences should be the focus of study in systematic arguments. Size variation is unlikely to justify the splitting of any hominin taxon.

Pattern of craniofacial dimorphism in *A. africanus*

What can be said about the pattern of craniofacial dimorphism in *A. africanus*? In some respects, *A. africanus* shows patterns common to all hominines. For example, size variation (represented by CVs) in the alveolar arch and palate is less than other facial dimensions. Further inferences about pattern rely strongly on the relationship of nonmetrical characters to size and reference to modern analogues. Perhaps unexpectedly, *A. africanus* displays two features of modern human sexual dimorphism: size-related variation in the form of the supraorbital region combined with the lack of apparent dimorphism in infraorbital concavity. *A. afri-*

canus also combines these with unique patterns of its own.

A prominent superciliary eminence does not occur in male or female apes but is present in larger *A. africanus* specimens. This implies that the human model of sexual dimorphism in the supraorbital and glabellar regions is more appropriate, as these are the most strongly dimorphic features of the modern human face. Dimorphism in the great ape supraorbital region is based mainly in the thickness of the supraorbital arch, which is also somewhat variable in *A. africanus*. Only Sts 5 and Stw 505 express typically male characters in both supraorbital and glabellar morphology, and according to these regions they are the best candidates for male *A. africanus* (which is somewhat inconsistent with the size of Sts 5). On the other hand, Sts 71 is probably female to judge by any character of the supraorbital region. Sts 17, Stw 13, and TM 1511 are of intermediate or unknown morphology, in part due to poor preservation.

Although the pattern of supraorbital variation compares well to modern humans, this does not automatically imply that *A. africanus* resembles early *Homo* in this respect. The features of *A. africanus* males do compare well with the form in KNM-ER 1470, but females of *A. africanus* do not possess the distinct supraorbital tori of small *H. habilis*. This may be due to systematic differences between KNM-ER 1470 and the other *Homo* specimens (Wood, 1991, 1992; Rightmire, 1993).

The other area in which *A. africanus* superficially resembles modern humans is the probable lack of dimorphism in the concavity, or hollowing, of the infraorbital region. The difference between chimpanzees and humans in this regard probably relates to the size of the canine root and its influence on the topography of the infraorbital region. Most specimens of *A. africanus* have slightly concave infraorbital regions. As canine crown-size dimorphism in *A. africanus* is considered to be low (Kay, 1982; Leutenegger and Shell, 1987; Kimbel and White, 1988; Plavcan and van Schaik, 1997), *A. africanus* may share with modern humans reduced dimorphism of canine size and related features of the maxilla. It is

unclear, however, that this reduced dimorphism could be called homologous when structural aspects of the maxilla of *A. africanus* are so different from humans. In broader comparisons of modern hominines (such as between lowland and mountain gorillas), there are clearly other factors in the form of the infraorbital region. In *A. africanus*, the concavity of the infraorbital region may be generally restricted by the pneumatization of the maxilla and zygomatic bone, the form of the anterior pillar, or a combination of these.

In the contours of the central face, anterior prominence of the zygomatic bone does give a few male gorillas a central facial hollow. It is also evident that the available males of *A. boisei* (OH 5, KNM-ER 406) have somewhat more hollowed faces than females (KNM-ER 732, KNM-ER 17400). Among *A. africanus* specimens, however, Sts 71 and probably MLD 6 have the most hollowed central faces, and that of Stw 505 is flat. Sts 5 has the most prominent nasal area, while other specimens are weakly prominent. Thus, unlike the condition in *A. boisei*, there does not appear to be any correlation between variation in central facial hollowing and craniofacial size, so it is unlikely that central facial hollowing or prominence is sexually dimorphic in *A. africanus*.

Further discussion of sexual dimorphism in facial morphology requires consideration of previous work by Rak (1983, 1985b). Rak reasoned that male primates typically express more derived characters than females and, in a sense, foreshadow descendant species. He specifically hypothesized that males of *A. africanus* should resemble *A. robustus* more than do females of *A. africanus*. This hypothesis was based on his proposed morphocline which had *A. africanus* phylogenetically intermediate between *A. afarensis* and *A. robustus*. If Rak's hypothesis of sexual dimorphism were correct, males of *A. africanus* should more frequently possess features such as anterior pillars, flat naso-alveolar clivuses, and central facial hollows. In this context, Rak (1983) assigned male status to Sts 5, Sts 71, and TM 1511, among others, and suggested that TM 1512 and Sts 52 are females. It has been pointed out, however, that putative sex differences among these

specimens are inconsistent with trends displayed by other primates, especially in traits such as alveolar prognathism (Kimbel and White, 1988).

The anterior pillar played an important role in Rak's phylogenetic considerations, it being seen as one of the derived features linking *A. africanus* and *A. robustus*. Rak (1985a:281) went so far as to say, "The presence of anterior pillars in the face of [*A. africanus*] places it clearly in the robust australopithecine clade," although not all specimens of *A. africanus* possess them. Specimens of *A. africanus* in which the anterior pillar is absent were suggested to be females and/or immature.

Of the four individuals without an anterior pillar, two are immature to some extent (Sts 52, Stw 498) and a third is of unknown developmental age (Stw 391). Thus, Rak's argument about the lack of a pillar in immature specimens has some support. As for females, it is true that the only adults to lack anterior pillars are relatively small (TM 1512 and possibly Stw 391). However, specimens of such disparate sizes as MLD 6, Sts 5, Sts 17, and Stw 505 at Sterkfontein possess anterior pillars. Sexual dimorphism may only be apparent in that a few females lack the feature. This would be somewhat analogous to the distribution of some great ape characters, such as the curvature of the infraorbital surface in lowland gorillas, where a few females lack a character otherwise possessed by most individuals.

The form of the anterior pillar may be more important than simply its presence or absence. It is true that the pillar is broader and less clearly distinguished from the infraorbital region in larger specimens (MLD 45, TM 1511, Stw 505, and probably MLD 9). This is also the case with Sts 71, which is a smaller cranium, but, given patterns in modern hominines, some overlap between sexes would be expected for any character. The strength of this argument depends to some extent on how specimens are classified, for Sts 5 and Stw 13 have much narrower and prominent anterior pillars. The sex of these specimens is in doubt.

Whether or not the form of the pillar is sexually dimorphic, the larger specimens of *A. africanus* still do not come to resemble *A. robustus*, as they lack several of the

peculiarities of the latter species (e.g., Rak's maxillary fossula and subforamen divide). This is in large part due to the fact that the pillar is not an isolated feature. Most importantly, *A. africanus* is almost certainly not dimorphic in the position of the zygomatic process (neither are modern hominines). The position of the zygomatic process plays an important role in creating the complex form of the infraorbital region of *A. robustus*, as outlined by Rak (1983). Lacking a more anteriorly positioned zygomatic process, males of *A. africanus* are unlikely to show the infraorbital form of *A. robustus*. It is also apparent that, when the face as a whole is considered, Sts 71 still bears the most striking resemblance to specimens of *A. robustus*. Compared to a greater range of specimens, Sts 71 now appears to be female. On the other hand, Stw 505 clearly demonstrates that males of *A. africanus* exaggerate the features of smaller specimens rather than take on the characteristics of more derived species.

Because the pattern of variation in adults of *A. africanus* can be accommodated with models of dimorphism based on extant analogues, this study is consistent with the view that the hypodigm does represent one species. To the extent that patterns of sexual dimorphism may be relevant to the phylogenetic position of *A. africanus*, it is important to note that the "derived" characteristic may be the pattern of sexual dimorphism itself. Particularly in the division of the supraorbital arch into superciliary and supraorbital components and the prominence of the superciliary eminence, Stw 505 and other putative males of *A. africanus* resemble modern humans. Thus, while the degree of dimorphism in *A. africanus* remained relatively high compared to later hominines, this species already possessed some aspects of the structural pattern of modern human craniofacial dimorphism.

SUMMARY AND CONCLUSIONS

The analysis of sexual dimorphism in the faces of modern hominines suggests certain patterns common to all species, despite great variance in the degree of dimorphism. Modern humans show a unique pattern of dimor-

phism in quantitative comparisons as well as morphological. Humans combine sexual dimorphism in the supraorbital region with a lack of dimorphism in the topography of the infraorbital region. Chimpanzees show the reverse pattern, with gorillas being more similar to chimpanzees than humans.

It is improbable that the size range of the *A. africanus* face could be sampled from populations of humans or chimpanzees, but the same size range occurs in samples of gorillas most of the time. Thus, the degree of size variation in the face of *A. africanus* was intermediate between those of less dimorphic and of more highly dimorphic modern hominines. This conclusion is the same whether specimens from Sterkfontein alone or from both Sterkfontein and Makapansgat are considered.

A combination of size and morphology suggests the following sex assignments for *A. africanus*: males—Stw 505, TM 1511, MLD 45, MLD 9; indeterminate—Sts 5, Stw 13; females—Sts 17, Sts 71, MLD 6, Sts 53, Sts 73, Sts 63, TM 1512. Among previous authors, the most similar conclusions were those of Broom (Broom and Schepers, 1946; Broom et al., 1950), who considered TM 1511 to be the only male among the first specimens he recovered. Different methods of estimating the degree of dimorphism among these specimens show that the faces of males of *A. africanus* are between 10 and 14% larger than those of females, corroborating the analysis of size variation by resampling.

Examination of other fossil hominin taxa indicates that the degree of sexual dimorphism in the *A. africanus* face is not exceptional. *A. boisei* is somewhat more sexually dimorphic than *A. africanus* and is more similar in this respect to gorillas. If the remains attributable to *H. habilis* represent one species, this species shares with *A. africanus* a moderately high level of sexual dimorphism. In no early hominin species considered here does the range of craniofacial size appear to be so great that it justifies division of the sample into two species.

Craniofacial morphology allows discussion of the pattern of dimorphism in *A. africanus*. In several characters of the face, including the presence of the anterior pillar, the hollowing of the central face, and the

concavity of the infraorbital region, males and females correspond to one another. Depending on how specimens are sexed, males may show broader anterior pillars that are less distinct from the infraorbital region. In addition, *A. africanus* is probably dimorphic in the form of the supraorbital region and particularly the prominence of the superciliary eminence. The latter indicates some aspects of modern human craniofacial dimorphism. Thus, both the degree and pattern of craniofacial dimorphism in adults of *A. africanus* are consistent with the interpretation of this hypodigm as a single species.

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APPENDIX. Definitions of measurements listed in Table 2¹

Facial heights

1. Orbital height, ORBH, M. 52: maximum distance from the superior to the inferior orbital margin, perpendicular to the orbital breadth (Fig. 1a)
2. Glabellar height, *GLAH*: glabella to prosthion,⁴ used as an additional measure of upper facial height for those specimens in which the position of nasion is unclear (Fig. 1c)
3. Upper facial height, UPFH, adjusted from M. 48: nasion to prosthion (Fig. 1c)
4. Nasal height, NASH, M. 55: nasion to nasospinale (Fig. 1a)
5. Orbito-alveolar height, OALH, M. 48(3): minimum distance from the inferior orbital margin to the alveolar margin (Fig. 1a)
6. Orbito-jugal height, *OJUH*: minimum distance from the inferior orbital margin to the alveolar margin of the maxilla between the canine and third premolar (Fig. 1c); the inferior terminus of the measurement is the same as that used for anterior maxillo-alveolar breadth and postcanine maxillo-alveolar length
7. Foraminal height, *FORH*: minimum distance from the superior margin of the infraorbital foramen to the maxillary alveolar margin (Fig. 1a); when multiple infraorbital foramina are present in a given specimen, the major foramen is used; if multiple foramina are of similar size, the average of their heights is taken to provide a single value for statistical purposes
8. Malar depth, MALH (Wood, 1991): minimum distance from the inferior orbital margin to the inferior margin of the zygomatic arch (Fig. 1a)
9. Alveolar height, ALVH, adjusted from M. 48(1): nasospinale to prosthion (Fig. 1a)

Facial breadths

10. Orbital breadth, ORBB, M. 51: maxillofrontale to ectoconchion (Fig. 1a)
11. Superior facial breadth, SUFB, M. 43: left frontomale temporale to right frontomale temporale (Fig. 1a). Equivalent to outer biorbital breadth
12. Anterior interorbital breadth, ITOB, M. 50: left maxillofrontale to right maxillofrontale (Fig. 1a)
13. Bimaxillary breadth, BMAB, M. 46: left zygomaxillare to right zygomaxillare (Fig. 1a)
14. Bizygomatic breadth, ZYGB, M. 45: zygion to zygion (i.e., the maximum breadth across the zygomatic arches in the same coronal and horizontal planes) (not illustrated)
15. Interforaminal breadth, *IFOB*: minimum distance between the medial margins of the left and right infraorbital foramina (Fig. 1a); specimens with multiple foramina are measured as described for foraminal height
16. Nasal aperture breadth, NASB, M. 54: maximum distance between the lateral margins of the nasal aperture in the same horizontal plane (Fig. 1a)
17. Snout breadth, *SNOB*: distance between the lateral margins of the canine buttresses (or anterior pillars, where appropriate) at the level of the inferior nasal margin (Fig. 1a); the measurement is not taken in modern humans

Maxillo-alveolar and palatal measurements

18. Anterior maxillo-alveolar breadth, ANMB, M. 61(2): distance between the alveolar margins of the maxillae, measured at the outer margin of the septum between the canine and third premolar on either side (Fig. 1b)
19. Maxillo-alveolar breadth, MAXB (Flower 1881), adjusted from M. 61: distance between the most lateral points on the alveolar margins of the maxillae at the midpoint of the second molar (Fig. 1b); this differs from the definitions of Martin and Knußmann (1988) and Wilder (1920), wherein the measurement is taken between the ectomolaria, which are the most lateral points but not always at the level of the second molar
20. Anterior palatal breadth, APAB, M. 63(2): distance between the lingual alveolar margins of the palate, measured at the most medial point on the septum between the canine and third premolar on either side (Fig. 1b)
21. Palatal breadth, PALB, adjusted from M. 63: distance between the lingual alveolar margins of the palate at the midpoint of the second molar (Fig. 1b)
22. Maxillo-alveolar length, MAXL, adjusted from M. 60: distance from prosthion to the midpoint of a line across the palate and alveolar processes at the level of the outer surface of the interalveolar septa between the second and third molars (Fig. 1b); the value is calculated by triangulation from two measurements: 1) the measurement of the distance between the left and right outer interalveolar septa (not the same as the maxillo-alveolar breadth described above) and 2) the distance from prosthion to the midpoint of the outer interalveolar septum
23. Postcanine maxillo-alveolar length, *PMXL*: distance from the outer surface of the interalveolar septum between the canine and third premolar to the corresponding point between the second and third molar on the same side (Fig. 1c)

Facial projections (Bilsborough and Wood, 1988; Wood, 1991)

24. Glabellar projection, GLAP: distance between glabella and the biporionic line in the median sagittal plane (Fig. 1c); the value of this measurement was determined by triangulation; the biporionic breadth and the chord distance from glabella to porion were measured and then used for calculation of glabellar projection
25. Prosthion projection, PROP: distance between prosthion and the biporionic line in the median sagittal plane, calculated as for glabellar projection (Fig. 1c)
26. Zygomaxillare to porion distance, ZYMP: distance from zygomaxillare to porion (Fig. 1c)
27. Zygomatic process to porion distance, MALP: distance from porion to the anterior limit of the zygomatic process (Fig. 1c)

Other measurements

28. Postorbital breadth, POSB, M. 9(1): maximum breadth across the greatest postorbital constriction of the frontal bones (Tobias, 1991, after Pycraft, 1928) (not illustrated); in humans this measurement is equivalent to the least frontal breadth (frontotemporale to frontotemporale) and was measured as such (Martin and Knußmann, 1988)

¹ If there has been a previous use, it is cited following each measurement abbreviation. Italics indicate a new measurement. "M." numbers refer to measurements in Martin and Knußmann (1988). Note that for all measurements using prosthion (*GLAH*, *UPFH*, *ALVH*, *MAXL*), prosthion is defined as the most anterior point on the alveolar margin of the maxilla in the median sagittal plane (Pearson, 1925; Howells, 1973), which differs slightly from the definitions of Tobias (1967, 1991) and Martin and Knußmann (1988). If the bone between the incisors slopes continuously forward, the alveolar margin is estimated relative to its position along the rest of the alveolar process.

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